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July 1999

Synopsis of Biological Data on the Nassau Grouper, *Epinephelus striatus* (Bloch, 1792), and the Jewfish, *E. itajara* (Lichtenstein, 1822)

Yvonne Sadovy
Anne-Marie Eklund

FAO Fisheries
Synopsis 157

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Synopsis of Biological Data on the Nassau Grouper, *Epinephelus striatus* (Bloch, 1792), and the Jewfish, *E. itajara* (Lichtenstein, 1822)

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ABSTRACT

Information on the biology, fishery resources, exploitation patterns, management, and conservation status of two species of grouper—the Nassau grouper, *Epinephelus striatus*, and the jewfish, *Epinephelus itajara*—is compiled, reviewed, and analyzed.

Introduction

The Nassau grouper, *Epinephelus striatus*, and the jewfish, *E. itajara*, are two important and conspicuous members of reef communities throughout the western Atlantic and Caribbean. These species are found from inshore to about 100 m in reef, mangrove, seagrass, and estuarine habitats. They are large, long-lived predators exceeding 800 mm (the Nassau) and 2,000 mm (the jewfish) in length and living three or four decades. They prey on a wide diversity of fishes and invertebrates. The sexual pattern of the Nassau grouper is primarily gonochoristic (separate sexes) thereby differing from the protogynous hermaphroditism (female to male sex change) more typical of groupers. The sexual pattern of the jewfish has not been confirmed.

Both species, but particularly the Nassau grouper, are of significant commercial and recreational interest, taken primarily by handline, fish trap, and speargun. In many insular areas, the Nassau grouper was once among the most abundant fishery species. However, since the 1970s, landings, mean sizes, and catch per unit of effort have all fallen sharply for both groupers in regional fisheries, and growth and recruitment overfishing are suspected or severe in some places. Spawning stock biomass per recruit has been estimated at close to 1%, far below the recommended minimum of 30%. Because of their large average sizes and ages at sexual maturity—400–450 mm TL, 4+ years, Nassau grouper, and 1100–1200 mm TL, 5+ years, jewfish—relative to other fishes in the multi-species fisheries targeted in the region, both species are often taken as juveniles. Nassau grouper, for example, recruit into the fishery well before attaining sexual maturity; capture age averages 2–9 years, which is young for a species that can attain 29 years or more. Large individuals of both species are particularly sought by recreational spearfishers, and reproductively active adults are often taken from spawning aggregations. The jewfish is now rare where formerly it was abundant and both species are commercially extinct for fishery purposes throughout significant portions of their ranges.

The fact that such long-lived, slow-growing fishes are extremely susceptible to fishing has long been recognized, and species that aggregate at specific times and

locations to spawn are particularly vulnerable (e.g. Polovina and Ralston, 1987; Bohnsack[1]). The Nassau grouper and jewfish assemble to spawn at specific times and locations in aggregations numbering as many as tens of thousands of individuals in the Nassau grouper and tens to one hundred, or more, individuals in the jewfish. The aggregations last only a few weeks each year and represent most, if not all, of the total annual reproductive effort for both species. Between 60 and 80 Nassau grouper aggregations have been identified, many exploited since at least the turn of the century. All, with the notable exception of Bermuda, are within the latitudinal range of 15–26° N. Heavy fishing has had such a severe impact on many of these aggregations that about one-third of them no longer form at traditional sites. Of particular note are the almost complete loss of aggregations from Cuba and the Greater Antilles, and declines in aggregations in the Bahamas. Similarly, of the few jewfish aggregations identified, one quarter no longer form. The evidently specific nature of the spawning sites means that adults may be habitat-limited to some extent, dependent for reproduction on aggregation sites which could represent critical bottlenecks in the life histories of these species.

There may also be specific times and places for very early life history phases of these two groupers. The time period over which settlement occurs in Nassaus, when larvae leave the plankton and colonize the substrate, appears to be brief, lasting but days each year. Such a short annual larval settlement period may increase vulnerability to short-term adverse weather conditions, to poor recruitment years, or when adult population levels are low. For early post-settlement fish, nursery areas may be quite specific. After settlement, the apparent importance of macroalgae and seagrass beds to juvenile Nassau grouper, and of mangroves to jewfish, may limit suitable nursery habitat for young fish of these species. Indeed, in reef fishes in general, suitable settlement habitat appears to be an important factor in enabling young, vulnerable fishes to avoid predation.

The conservation status of the Nassau grouper and the jewfish is precarious in some areas. Standard fishery management approaches such as quotas and size limits are not effective for larger reef species in multi-species fisheries. The greatest protection for such species is likely afforded by restrictions or elimination of gear and effort, especially over spawning aggregations, to protect spawning biomass. Marine reserves can protect both juvenile and adult biomass and, if properly placed, the critical habitats on which they may depend. Indeed, some recoveries in both species may already have occurred from protection. Nonetheless, both species are in urgent need of management throughout much of their geographic ranges. In 1996, both species were included on the "Red List" of the International Union for the Conservation of Nature and both are candidates for the United States Endangered Species List. Moratoriums are now in effect for the Nassau grouper and jewfish in all waters of the United States and Bermuda. Aquaculture and stock enhancement initiatives are promising but are not solutions to overfishing nor are they excuses not to manage.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

***Epinephelus striatus* (Bloch, 1792) (Fig. 1)** Nassau grouper, *Epinephelus striatus* (Bloch, 1792). Original description as *Anthias striatus* Bloch, 1792:6:125, pl. 324 (type locality; Atlantic Ocean) (Smith, 1971; Heemstra and Randall, 1993). The name comes from the Greek *Epinephelus*, meaning clouded over, in reference to the membrane believed to cover the eye of *Epinephelus ruber* (*Mycteroperca rubra*) (Smith, 1971) and the Latin, *striatus*, provided with stripes, in reference to the color pattern.

***Epinephelus itajara* (Lichtenstein, 1822) (Fig. 2)** Jewfish (formerly giant grouper), *Epinephelus* (*Promicrops*) *itajara* (Lichtenstein, 1822). Original description as *Serranus itajara* Lichtenstein, 1822:278 (type locality: Brazil) (Smith, 1971; Heemstra and Randall, 1993). The derivation of *itajara* is unclear.

1.12 Synonymy

The following primary synonymies are based on Heemstra and Randall (1993) and Heemstra[2]. For full synonymy see Smith (1971); see also Bullock and Smith (1991) for *E. itajara.*

Epinephelus striatus

Anthias cherna Bloch and Schneider, 1801

Serranus gymnopareius Valenciennes *in* Cuvier and Valenciennes, 1828

Epinephelus itajara

? *Serranus mentzelii* Valenciennes *in* Cuvier and Valenciennes 1828

[1] Bohnsack, J. A. 1989. Protection of grouper spawning aggregations. Coastal Resources Division Contr. No. 88-89-06, 8 p.

[2] Heemstra, Phillip. 1993. J.L.B. Smith Institute of Ichthyology, Private Bag 101 Grahamstown, 6140 South Africa. Personal commun.

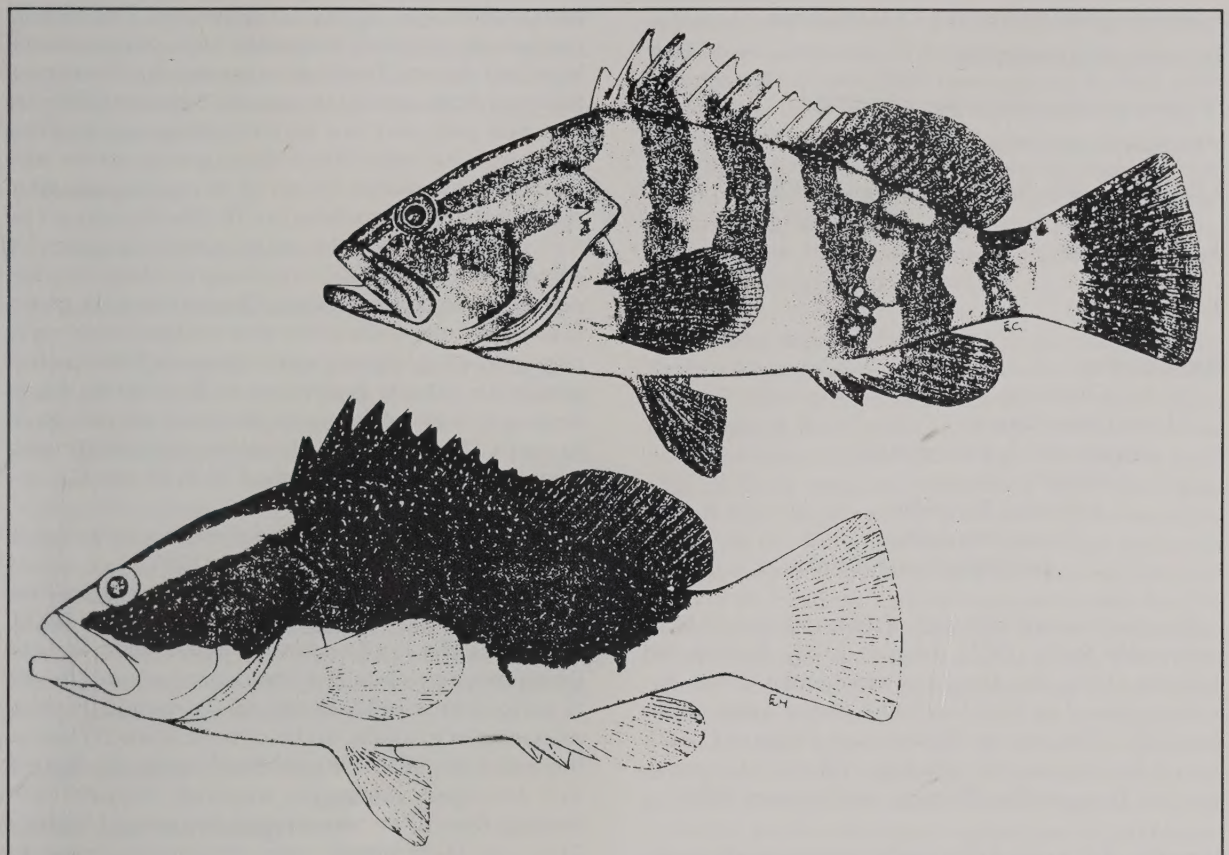

Figure 1
Nassau grouper, *Epinephelus striatus*, adult, showing external morphology; upper shows normal coloration while lower shows the bicolor form seen at spawning aggregations and during some intraspecific interactions (redrafted from Heemstra and Randall, 1993).

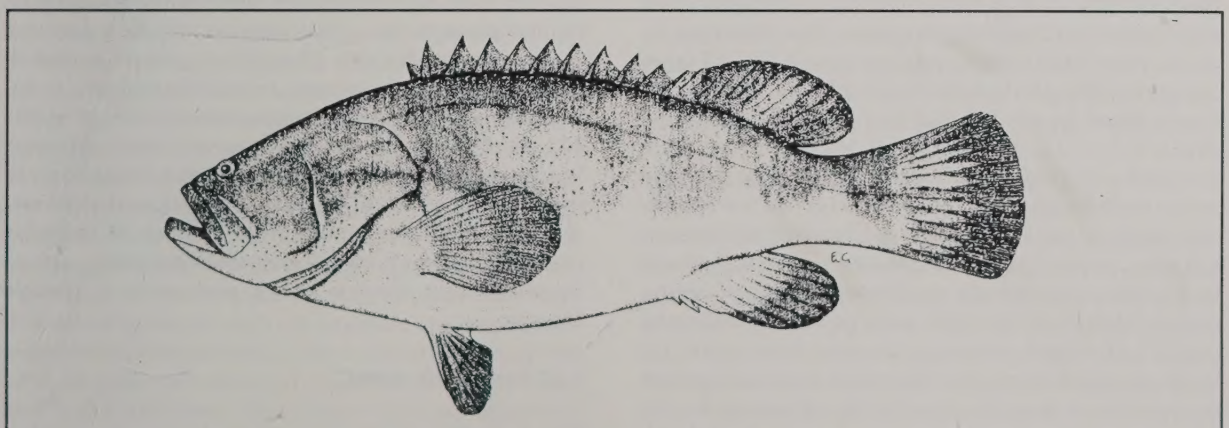

Figure 2
Jewfish, *Epinephelus itajara*, adult, showing external morphology (redrafted from Heemstra and Randall, 1993).

? *Serranus galeus* Müller and Troschel, 1848

Serranus guasa Poey, 1861

Serranus quinquefasciatus Bocourt, 1868

? *Promicrops esonue* Ehrenbaum, 1914

? *Promicrops ditobo* Roux and Collignon, 1954

1.2 Taxonomy

1.21 Affinities

Suprageneric

Phylum Chordata
Class Osteichthyes
Superorder Acanthopterygii
Order Perciformes
Suborder Percoidei
Family Serranidae
Subfamily Epinephelinae

Systematics and distribution of the groupers have been reviewed by Smith (1971), Johnson (1983), Baldwin and Johnson (1993), and Heemstra and Randall (1993). Systematics based on larval serranids were carried out by Kendall (1979) and by Baldwin and Johnson (1993). Larval features provide the only evidence of a monophyletic Epinephelini (Baldwin and Johnson, 1993).

Generic For a comprehensive synonymy see Heemstra and Randall (1993) from which the following description was taken.

Genus *Epinephelus* Bloch, 1793. *Epinephelus* is the most speciose genus of the subfamily Epinephelinae which comprises a number of large to very large sea basses that are the most common top level predators on coral reefs. Body elongate, robust (subcylindrical), oblong or deep and compressed; body depth greater than, subequal to, or less than, head length and contained 2.3 to 3.7 times in standard length (SL), the body width 1.8 to 2.8 in the depth. Head length 2.1 to 2.8 times in SL; preorbital depth 6.7 to 15 times in head length; preopercle rounded or angular, the posterior edge serrate, with the serrae at the angle more or less enlarged; a few species with small serrae (mostly covered by skin) on the ventral edge; canines present at front of jaws, but they may be small in some species; no distinctly enlarged canine teeth at midside of lower jaw; teeth present on palatines; maxilla of adults without a distinct bony knob on ventroposterior corner, but there may be an abrupt step or hook-like process (covered by the upper lip) on the distal part of the ventral edge; supramaxilla well developed. Dorsal fin usually with XI spines and 12 to 19 rays, the fin origin above the opercle; length of base of soft-rayed part of dorsal fin not more than base of spinous part; anal fin with III distinct spines and 7 to 10 rays; pectoral fin rounded, the middle rays longest; caudal branched rays and 7 to 10 procurrent rays in lower part. Scales on body ctenoid or smooth. Supraneural bones 2; dorsal and anal fins without trisegmental pterygiophores; rear edge of first dorsal pterygiophore with or without excavation for tip of second neural spine; epipleural ribs on vertebrae 1 to 10. The diversity of cranial morphology of the many species assigned to *Epinephelus* makes it difficult to recognize diagnostic cranial characters for the genus. Characters of the larvae (Leis, 1986): pelvic-fin spines with 4 ridges; supraocular ridge with a single strong spine; spines on lower limb of preopercle serrate; posterior 1 or 2 dorsal-fin spines develop first as soft rays and all spines are present in larvae of 13.5 to 16 mm; all anal-fin spines are present prior to settlement at a length of 16 to 18 mm SL.

Specific The following diagnoses are from Smith (1971) and Heemstra and Randall (1993):

Epinephelus striatus Gill rakers 8 or 9 on upper limb and 15 to 17 on lower limb, total 23 to 26. Dorsal fin XI, 16–18 rays, the third or fourth spine longest and the interspinous membranes distinctly notched; anal fin, III, 8; pectoral-fin rays 17–19; caudal fin rounded in juveniles, convex in adults. Scales ctenoid, about 50 lateral-line scales and 98 to 108 lateral-scale series. Skull crests well developed, convergent anteriorly. Supraethmoid forming floor of pit between anterior ends of frontals. There are 21–25 pyloric caeca. Proportional measurements of 10 specimens are given in Table 7 in Smith (1971).

Epinephelus itajara Gill rakers 8 or 9 on upper limb and 13 to 15 on lower limb, total 21 to 24; gill arches covered with small bony plates. Dorsal fin XI spines and 15–16 rays, the spines short, 3rd to 11th subequal and shorter than the first ray, the membranes distinctly indented between the spines; anal fin with III spines and 8 rays; pectoral-fin rays 18 or 19; caudal fin rounded. Body scales strongly ctenoid; lateral-line scales 61 to 64, each with 4 to 6 radiating ridges; lateral-scale series 89–112. Skull crests low with frontoparietal crests converging anteriorly. Supraethmoid expanded transversely to form wall anterior to frontals. Proportional measurements of 10 specimens are given in Table 20 in Smith (1971). *E. itajara* is one of only two *Epinephelus* species found in both eastern Pacific and western Atlantic Oceans.

1.22 Taxonomic status

The distinctive color pattern of the Nassau grouper has spared it from the nomenclatural confusion of less easily recognizable species (Smith, 1971). Smith (1971) demoted the genus *Promicrops*, containing *E. itajara* and

E. lanceolatus, to a subgenus of *Epinephelus*, stating that the two species in *Promicrops*, although highly specialized and distinctive, were clearly allied with other species of *Epinephelus*. Heemstra and Randall (1993) concur with this opinion.

1.23 Subspecies

No subspecies are recognized.

1.24 Standard common names, vernacular names

The word "grouper" comes from the Portuguese "garrupa" probably derived from a similar sounding name that South American natives used for large groupers. The Nassau grouper is variously known as: Hamlet (Bermuda); Merou rayé (French); Cherna criolla (Cuba); Mero cherna (Puerto Rico); Mero gallina, mero batata (Venezuela) (Erdman, 1987; Butler et al., 1993; Heemstra and Randall, 1993; Cervigón, 1994). The jewfish is variously known as Merou géant (French); Mero guasa (Colombia); Mero (Brazil); Cherna (Mexico); Cherne (Peru); Mero sapo (Puerto Rico); June fish (Colombia); Guasa (Venezuela) (Thompson, 1945; Erdman, 1987; Heemstra and Randall, 1993).

1.3 Morphology

1.31 External morphology

The following descriptions are based predominantly on Smith (1971) and Heemstra and Randall (1993).

Epinephelus striatus The Nassau grouper is a moderate-sized *Epinephelus* with large eyes and a robust body (Fig. 1). Body depth distinctly less than head length, depth contained 2.6 to 2.9 times in SL (for fish 160 to 330 mm SL). Head length contained 2.4 to 2.6 times in SL; interorbital convex; preopercle evenly serrate, without salient angle; posterior nostrils somewhat enlarged and elongated or comma-shaped in large adults. Ground color generally buff, with 5 dark brown vertical bars and a large black saddle blotch on top of caudal peduncle; a row of black spots below and behind eye. Distinctive dark tuning-fork mark beginning at front of upper jaw, extending dorsally along interorbital region, and bifurcating on top of head behind the eyes; another dark band from tip of snout through eye and then curving upward to meet its fellow just before dorsal-fin origin. Some fish have irregular pale spots and blotches all over the head and body; specimens from deep water are somewhat pinkish or reddish ventrally. The inside of the mouth is red, the teeth are caniniform and villiform and are in two series in each jaw (Smith, 1978). The range of color is wide (Section 3.16). Color pattern can change within minutes from almost white to bicolored to uniformly dark brown, according to the behavioral state of the fish (Longley, 1917; Colin, 1992; Heemstra and Randall, 1993; Carter et al., 1994). A distinctive bicolored pattern (Fig. 1) is seen when two adults or an adult and large juvenile meet and is frequently observed in spawning aggregations (Section 3.16) (Heemstra and Randall, 1993). Only dots around the eyes and the blotch on the caudal peduncle do not change (Smith, 1971). Juveniles exhibit a color pattern similar to adults (e.g. Silva Lee, 1977).

Epinephelus itajara The jewfish is the largest of the western North Atlantic groupers, readily distinguishable from all other species by its nearly terete shape, short dorsal spines, short canine teeth and distinctive coloration; head extremely broad and flat, eyes relatively small (Fig. 2). Body elongate, the greatest width more than half of body depth, which is distinctly less than head length (in fish 150 to 1600 mm); body depth contained 2.7 to 3.4 times in SL. Head length contained 2.3 to 2.9 times in SL; head extremely broad; interorbital flat, the width equals eye diameter in fish 100 to 150 mm SL; distinctly greater than eye diameter in fish 180 to 250 mm SL, and 1.5 to 3.4 times greater than eye diameter in fish 300 to 1600 mm SL; eye diameter contained 5 to 8 times in head length for fish 100 to 300 mm SL and 8 to 13 times in head length for fish 350 to 1600 mm SL; preopercle rounded, finely serrate; nostrils round, subequal; maxilla scaly, reaching well past eye; midlateral part of lower jaw with 3 to 5 rows of subequal teeth; no canines at front of jaws. Scales ctenoid and rugose in adults. Body color is brownish yellow, or may be grey or greenish. The head and the dorsal part of the body and fins have small black spots, which get smaller with growth. Fish as small as 87 mm SL are greenish or tawny, have 3 or 4 faint, irregular, subvertical dark bars posteriorly on body and another covering rear half of caudal peduncle. They have longer dorsal spines and more vivid coloration but otherwise do not markedly differ from adults (Bullock and Smith, 1991). There is no saddle-like blotch on the caudal peduncle (Rivas, 1964).

1.33 Protein specificity

Limited work on genetic variability in the Nassau grouper suggests that, while gene flow occurs throughout much of its geographic range, the relative contributions of local and foreign recruitment to particular populations have yet to be determined. Cellular DNA in the Nassau was reported to be 1.3 picograms (haploid), similar to that of other serranids and similar to the average value of a wide diversity of other percomorph fishes (Hinegardner and Rosen, 1972).

Hateley (in press) presented preliminary results on genetic variability in the Nassau grouper, based on en-

zyme electrophoresis. Clearly resolved enzyme phenotypes were obtained at 20 loci, of which 5 exhibited polymorphisms. On the basis of a sample of 264 individuals taken from Belize, Bahamas, Turks and Caicos and Cayman Islands, intermediate to low levels of genetic variability were indicated; mean heterozygosity per locus was 0.024; proportion of polymorphic loci = 0.15, and the mean effective number of alleles was 1.45. There was no evidence for population sub-structuring by sex or small-scale spatial distribution, nor for macrogeographic stock separation. The results were interpreted as being consistent with a single panmictic population within the northern Caribbean basin and suggested high gene flow in the region. However, since gel electrophoresis can detect only differences among samples and not similarities, it may not detect real inter-stock differences and more sensitive methods must be applied to increase resolution (Hateley[3]).

A study of genetic population structure in the jewfish and Nassau grouper, using PCR (Polymerase Chain Reaction)-amplified mtDNA genes and nuclear microsatellites, revealed no clearly defined population substructuring for either species at the geographic locations sampled, i.e. Belize, Cuba, Bahamas, Florida for Nassau, and Belize and Florida for jewfish (Sedberry et al.[4]). Although these data indicate that spawning aggregations are not exclusively self-recruiting and that the larval stages can disperse over great distances, this study does not allow a definitive evaluation of the relative importance of self-recruitment and larval immigration to local populations (Sedberry et al.[4]). Since the use of microsatellites is not confounded by environmental variables, their use represents a superior approach for examining stock structure compared to non-genetic approaches, such as otolith microchemistry (Patterson et al.[5]).

2 DISTRIBUTION

2.1 Total area

Epinephelus striatus The Nassau grouper is distributed in waters off Bermuda and Florida throughout the Bahamas and Caribbean Sea, down to southern Brazil (Smith, 1971; Acero and Garzon-Ferreira, 1991; Heemstra and Randall, 1993; Cervigón, 1994) (Fig. 3). To the west, it occurs off the Yucatan Peninsula, Mexico, at Arrecife Alacranes (north of Progreso) (Hildebrand et al., 1964). It is a rare or transient species in the Gulf of Mexico (Reed, 1941; Hoese and Moore, 1977) where it is replaced by *Epinephelus morio* (Smith, 1971).

The Nassau grouper is primarily a shallow water, insular species and, when mature, is most abundant in clear water with high relief coral reefs or rocky substrate; it occurs from the shoreline to at least 100 m and on both natural and artificial reefs (Smith, 1971; Beets and Hixon, 1994; Colin et al., 1997). Although it is fished to 130 m, greatest trap catches in the Leeward Islands were from 52–60 m (Brownell and Rainey, 1971). In Venezuela it is common to 40 m in the Archipelago Los Roques, but rare in northeastern islands (Cervigón, 1966).

Nassau grouper otoliths have been retrieved from a variety of sites (middens) in prehistoric fishing communities of the Caribbean, and the species represented an important component of these communities. Otoliths were relatively abundant at sites on eastern Antigua (AD 500–1150), in Grenada (AD 0–500, AD 1000–1500), San Salvador, Bahamas (AD 850–1100) St. John, Virgin Islands (AD 700–1200), Florida west coast (2000–1000 BC, AD 150–300, AD 400–1000), St. Lucia, West Indies (AD 0–1500) and on the north coast of Jamaica (no date) (Wing et al., 1968; Wing and Reitz, 1982).

Epinephelus itajara The jewfish occurs in tropical and subtropical waters of the Atlantic Ocean (Fig. 4), from Florida to Brazil down to São Paulo State, throughout the Gulf of Mexico, and in the Caribbean. It is also recorded from Bermuda (as *Promicrops itajara*) (Smith, 1959, 1961; Ferreira Padovani and Maida, 1995), although it is rare there, and is present in the eastern Pacific from the Gulf of California to Peru (Smith, 1971; Heemstra and Randall, 1993). It is common on the Campeche Bank off southern Mexico (Stewart, 1987) and is known from the isolated Isla de Aves (Brownell and Gúzman, 1974). It is also reported from the eastern Atlantic from Sénégal to the Congo but is rare in the Canary Islands (Heemstra and Randall, 1993). Heemstra and Randall doubt that jewfish of the eastern and western Atlantic and the eastern Pacific share a common gene pool, but could find no evidence, either in specimens examined or in the published literature, to confirm that different species are involved. Heemstra (1991), however, suggests that juveniles, with their predilection for estuarine and mangrove habitats, could easily traverse the Isthmus of Panama via the Panama Canal. This species was once common in Florida and in parts of the Gulf of Mexico but infrequently encountered in the West Indies (Randall, 1983).

Jewfish, in general, prefer holes, caves, or places where they can find shelter (Nagelkerken, 1981). Along the

[3] Hateley, Jon. 1994. Division of Fisheries, Department of Agriculture, Fisheries and Parks, P.O. Box CR 52, Crawl CR BX, Bermuda. Personal commun.

[4] Sedberry, G. R., D. E. Stevenson, and R. W. Chapman. 1996. Stock identification in potentially threatened species of grouper (Teleostei: Serranidae: Epinephelinae) in Atlantic and Caribbean Waters. Final Rep. MARFIN Grant No. NA47FF0012. South Carolina Dept. of Natural Resources, Marine Resources Research Institute. p. 51.

[5] Patterson, H. M., S. R. Thorrold, and J. M. Shenker. Analysis of otolith chemistry in Nassau grouper (*Epinephelus striatus*) from the Bahamas and Belize using solution-based ICPMS. Unpubl. manuscr., 24 p.

Figure 3
Geographic distribution (indicated by the solid line) of the Nassau grouper, *Epinephelus striatus*, in the western Atlantic (redrafted from Heemstra and Randall, 1993).

Florida west coast, this species ranges from shallow bays and estuaries to offshore, invading tidal streams on feeding forays (Odum et al.[6]). Large adults are found around high-relief ledges and offshore wrecks (Smith, 1976) and in shallow water in the Everglades, Florida Bay, and the Florida Keys (Bullock and Smith, 1991). The center of abundance of jewfish along the west coast of Florida appears to be in the vicinity of the Ten Thousand Islands (south of Naples), where extensive mangrove swamp habitat, suitable for juveniles, exists (Bullock and Smith, 1991). Jewfish otoliths were found from prehistoric fishing communities in Florida, but at no other sites surveyed in the Caribbean (Wing et al., 1968; Wing and Reitz, 1982).

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

Epinephelus striatus Eggs are released while fish are in spawning aggregations that form annually at highly specific sites and times (Sections 3.13 and 3.16). Spawning has not been recorded outside of spawning aggregations. About 60–80 aggregation sites are known, mostly from insular areas (Table 1, Figs. 5A and B), although many no longer form (Section 5.43).

Spawning aggregation sites typically occur near the edge of insular platforms, as little as 350 m from the shore, and close to a drop-off into deep water over a wide (6–50 m) depth range and diversity of substrate types. Sites are characteristically small, highly circumscribed areas, measuring several hundred meters in diameter, with soft corals, sponges, stony coral outcrops, and sandy depressions (Craig, 1966; Smith, 1972; Burnett-Herkes, 1975; Olsen and LaPlace, 1979; Colin et al., 1987; Carter, 1989; Fine, 1990; Beets and Friedlander, 1992; Colin, 1992; Aguilar-Perera, 1994).

Nassau grouper larvae are rarely reported from offshore waters (Leis, 1987) and little is known of their movements or distribution, other than limited data on

[6] Odum, W. E., C. C. McIvor, and T. J. Smith III. 1982. The ecology of the mangroves of southern Florida: a community profile. U. S. Fish Wild. Serv. Biol. Serv. FWS-OBS-81/24. 144 p.

Figure 4
Geographic distribution (indicated by the solid line) of the jewfish, *Epinephelus itajara,* in the western and eastern Atlantic and the eastern Pacific (redrafted from Heemstra and Randall, 1993).

settlement patterns. Currents in the vicinity of aggregation sites do not necessarily favor offshore egg transport, leaving open the possibility that some stocks are partially self-recruiting. For example, drogues (floats which drift with water currents) deployed near gametes at eastern Long Island, Bahamas, moved little from the shelf edge for several days immediately following spawning and one ended up inshore (Colin, 1992). Collections of pelagic larvae were made 0.8–16 km off Lee Stocking Island, Bahamas, at 2–50 m depths and from tidal channels leading onto the Exuma Bank (Greenwood, 1991). Inshore samples were taken during the day and offshore samples at night (Greenwood, 1991).

Small juvenile Nassau grouper are common in shallow seagrass beds, macroalgae, and around clumps of *Porites* spp. coral (Randall, 1983; Eggleston, 1995). Juveniles settle into the interstices of macroalgal clumps, remaining several months before associating with other microhabitats in macroalgal beds. Monthly repeated censuses of a cohort indicated that juvenile density decreased sharply after settlement, until fish emerged from algal habitat at several months of age, and thereafter remained relatively constant (Dahlgren, 1998). They are also found in deeper water banks and offshore reefs (Tucker et al., 1993; Colin et al., 1997) and recruit to artificial reefs (Beets and Hixon, 1994). Recently settled Nassau grouper were collected from tilefish, *Malacanthus plumieri,* rubble mounds at 18 m or associated with discarded queen conch, *Strombus gigas,* shells and other debris around *Thalassia* beds (Wicklund[7]). In the Bahamas, abundance of late-larval to early-juvenile Nassaus was substantially higher in macroalgae (mainly *Laurencia* spp.) than in seagrass, probably as a result of active selection for macroalgae to avoid high post-settlement predation in seagrass beds (Nadeau and Eggleston, 1996; Nadeau[8]). Juveniles shifted from the macroalgal habitat to natural and artificial patch reefs over a 3-month period at 120–150 mm total length (TL) (Eggleston,

[7] Wicklund, Bob. 1990. Caribbean Marine Research Center, Vero Beach Laboratory, 805 East 46th Place, Vero Beach, FL 32963. Personal commun.

[8] Nadeau, David A. 1996. MEAS Dept., North Carolina State University, Box 8208, Raleigh, NC 27695-8208. Personal commun.

Table 1A

Locations and contemporary status of Nassau grouper, *Epinephelus striatus*, spawning aggregations. Approximate number of aggregations known for each region is indicated in parentheses (modified from Sadovy, 1997; also Claro, text footnote 15; Thompson, text footnote 39; Ward, text footnote 45).

Region	Location	Status
Bahamas (23)	Andros Island	Heavily exploited
Bahamas	Long Island	Declines noted
Bahamas	Cat Cay/Bimini	Active but intermittent
Belize (6)	Cay Glory	Threefold decline over thirty years
Belize	Lighthouse Reef	Active
Belize	Ambergris Point	Disappeared
Bermuda (3)	Three sites	Disappeared
Cayman Islands (5)	Three major sites	Recent declines
SE Cuba (4)[1]	Cabo Cruz	Disappeared
SW Cuba	Cayo Cuano	Declining landings
NW Cuba	San Carlos	Disappeared
Dominican Republic (1)	Punta Rusia	Possibly disappeared
Honduras (1)	Bay Islands	Fiftyfold decline over three years
Mexico (7)	Majahual	Declines since the 1970s
Mexico	Xahuaxhol	Active
Puerto Rico (3)	Mona Island	Disappeared
Puerto Rico	S and SW coasts	Disappeared 1970-80s
U.S. Virgin Is. (3)	St. Thomas/St. Croix	Disappeared in 1970s/1980s
British Virgin Is. (4)	Status unknown	

[1] As many as 21 aggregations were noted in the 19th century in Cuba (Vilaro Diaz, 1884) although contemporary status is unknown (see Table 1B).

1995). On shallow artificial reefs in the Virgin Islands, 30–80 mm TL juveniles occupied small burrows beneath the reef while larger juveniles occupied holes in the reefs (Beets and Hixon, 1994). Schools of 30–40 juveniles (250–350 mm TL) were observed at 8–10 m depth in the Cayman Islands (Tucker et al., 1993).

Epinephelus itajara Off the southwest coast of Florida, groups of jewfish form periodically around shipwrecks, rock ledges and isolated patch reefs down to 45 m depths (Eklund, personal observ.). These aggregations are presumably for spawning, although actual spawning has not been observed. Off Hobe Sound, southeast Florida, an aggregation of 24 jewfish, which used to assemble in 5 m of water, no longer forms at this site (William Parks cited in Gulf of Mexico Fishery Management Council [GMFMC][9]). Historically, an aggregation occurred off Palm Beach, also southeast Florida, but that aggregation has also disappeared (South Atlantic Fishery Management Council [SAFMC][10]). Aggregations are known off Belize and Colombia (Section 3.16) (Fig. 6). Distribution of jewfish larvae is unknown.

Jewfish juveniles have been collected from inshore, shallow (2–3 m) habitats, including mangrove swamps, bulkheads and bridges, and in poorly oxygenated canals (Springer and Woodburn, 1960; Tabb and Manning, 1961; Lindall et al., 1975; Thompson and Munro, 1978; Bullock and Smith, 1991). Small young-of-the-year (46–88 mm SL) appear in grass beds and estuaries off Florida from November through January, indicating a summer spawning period (Bullock and Smith, 1991). In southwestern Puerto Rico, six larvae (14.7–17.9 mm SL) were taken in mangrove areas by night-light in mid-September 1988, indicating recent spawning (Dennis et al., 1991).

[9] Gulf of Mexico Fishery Management Council (GMFMC). 1990. Amendment Number 2 to the Fishery Management Plan for the Reef Fish Fishery of the Gulf of Mexico, 31 p.

[10] South Atlantic Fishery Management Council (SAFMC). 1990. Amendment Number 2, Regulatory Impact Review, Regulatory Flexibility Analysis and Environmental Assessment for Fishery Management Plan for the Snapper Grouper Fishery of the South Atlantic Region, 47 p.

Table 1B

Details of aggregation sites of *Epinephelus striatus* noted in Cuba and the Bahamas which, between them, include about 50% of all sites recorded. Unpublished sites in the Bahamas reported by fishermen and fishing vessel captains in 1992 (Source: Colin Higgs, Department of Fisheries, Government of the Bahamas). Sites and spawning times in Cuba were noted in the 19th century (Vilaro Diaz, 1884) although it has not been possible to verify which sites were the same as contemporary ones reported by Claro et al. (1990).

Location	Spawning site	Moon phase
Cuba		
Matanzas	Cayos Francés, Bahía de Cadíz	Full moon
Mantua	Cays and rocky areas	Between full and new moons
Bahía Honda	From Rancho del Obispo to Punta del Negro	Between full and new moons
Isla de Pinos	To the south, a mile from the reefs	Full moon
San Cayetano	From Cayo Blanco to Cayo Jutías	—
Coloma	—	Full moon
Cárdenas	Drop-off areas, especially Cayo Bahía de Cadíz and Mono Grande	Full moon
Habana	—	Between full and new moons
Cienfuegos	East of Cayos de Las Doce Leguas, Cayo Blanco de Sasa, Punta de Piedras, Los Jardines y Jardinillos, near shelf-edge	Between new and full moons
Puerto Padre	The entire district	Between full and new moons
Gibara	—	—
Nuevítas	Punta Rasa	Between full and new moons
Caibarien	Shelf-edge areas	Between full and new moons
Punta Alegre	From Cayo Francés to western Cayo Santa María	Full moon
Batabanó	All along the coast	Full moon
Mariel	Los Jardines and Jardinillos banks	Full moon
Manzanillo	—	Full moon
Baracoa	—	—
Guantánamo	—	—
Cuba	Specific banks	Between new and full moons
Sagua	—	Between new and full moons
Bahamas[1]		
Berry Islands	Off Little Harbour Cay, 6 miles west[2] of Little Stirrup Cay, Ginger Bread Ground, NE and SW of Great Isaac	Full moon
Bimini	Off Dollar Harbour, Cat Cay	Full moon
Andros	Off High Cay[2], off Tinker Rock[2], off South Rock, south of Green Cay, Sand Bores between Andros and Exuma	Full moon
New Providence	SW Reef	Full moon
Ragged Island	Double Breasted Cay	Full moon
Long Island	South End Point[2], North Side Place, north end opposite Stella Maris	Full moon
Cat Island	North side opposite Arthur's Town[2]	Full moon
Acklins	Off Castle Island light	Full moon
Eleuthera	Six Shillings Channel, Booby Rock Channel, Ship Channel, off Powell Point	Full moon
Exuma	Off Sail Rocks[2], North Exuma Cays	Full moon
Cav Sal	Off Anguilla Cays[2]	Full moon

[1] Best fishing at Bahamas sites is reported three days prior to and three days after full moon between November to January; this implies that full moon is probably the spawning period. Fig. 5B shows approximate locations of Bahamas sites.

[2] Indicates sites identified as the main aggregation sites by the Bahamas survey.

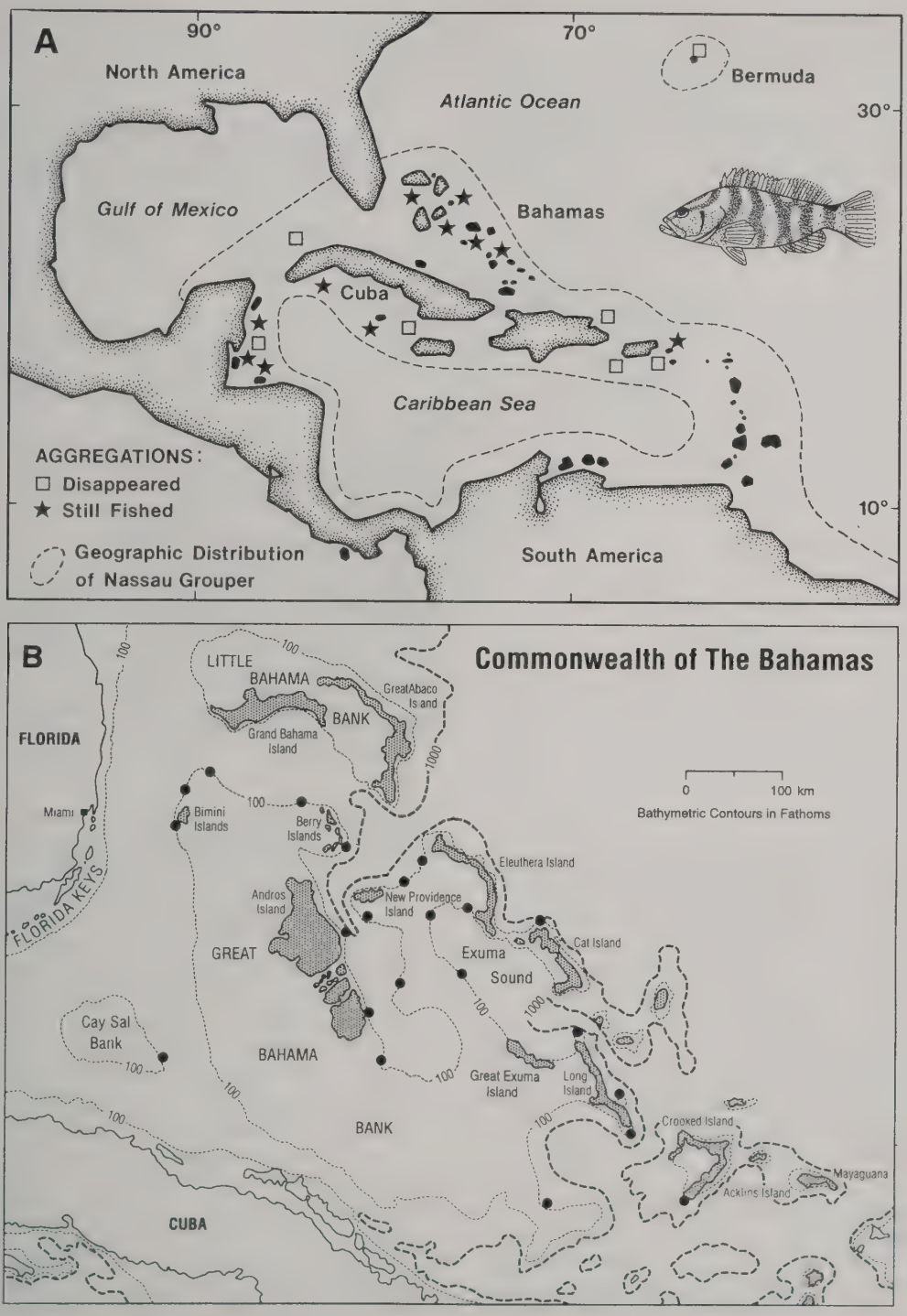

Figure 5

(A) Map indicating approximate locations of spawning aggregations of Nassau grouper, *Epinephelus striatus*, that are still fished (closed star) and which no longer form (square) throughout its geographic range. [Symbols may represent more than one aggregation in the general area indicated (updated from Sadovy, 1997 - see Table 1 for more details).] (B) Map indicating approximate sites (represented by black circles) of spawning aggregations in the Bahamas. See Table 1B for details.

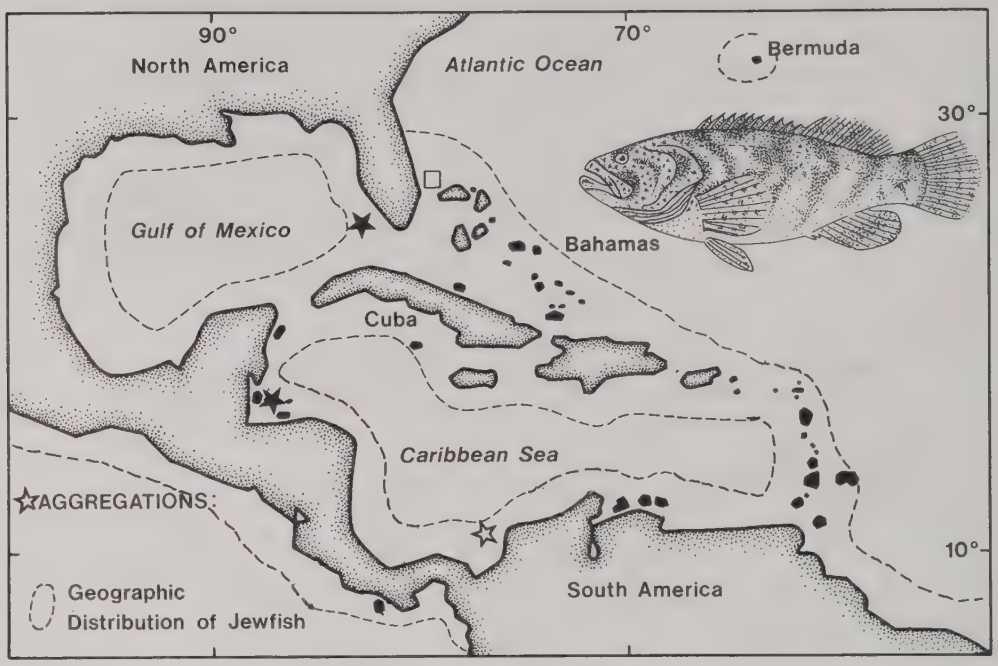

Figure 6

Map indicating approximate locations of spawning aggregations of the jewfish, *Epinephelus itajara*, that still have fish (closed star), for which current status could not be confirmed (open star), and which no longer form (square). The site(s) in SW Florida has not been fished since 1990.

2.22 Adults

Epinephelus striatus No general distinction can be made between adult and juvenile habitats, although a general size segregation with depth occurs with smaller fish in shallow inshore waters and larger individuals more common on deeper offshore banks (Bardach et al., 1958; Cervigón, 1966; Silva Lee, 1974; Radakov et al., 1975; Thompson and Munro, 1978). The extent to which this pattern is caused by greater fishing intensity inshore, or by differential movements of different-sized fish, is unknown. Adults lead solitary lives outside of the spawning season, rarely venturing far from cover (Böhlke and Chaplin, 1968; Smith, 1971; Carter et al., 1994; Sluka et al.,1998).

Epinephelus itajara Jewfish occur either as solitary individuals or in groups of up to 100 in shallow water, typically in less than 40 m water depth (Eklund, personal observ.). Zinkowski (1971), however, observed a group of 20–30 individuals in a 90 m-deep cave, and Carpenter and Nelson (1971) caught jewfish off Panama, western Colombia, and the Guianas down to 55 m during exploratory fishing in the Caribbean Sea. In Florida, this species is often taken around docks and bridges and on set-lines made fast to mangrove trees (Smith, 1971), while in Jamaica, large adults were once captured in Kingston Harbor (Thompson and Munro, 1978). Large jewfish are sedentary and exhibit little inter-reef movement; Smith (1976) observed the same individuals for more than a year at specific reef sites off Florida.

2.3 Determinants of distribution changes

Epinephelus striatus Primary determinants of distribution changes in Nassau grouper are not known although water clarity, habitat, and substrate type appear to be important (Smith, 1971; Eggleston, 1995). This species is most abundant in clear waters of high-relief coral or rocky reefs. Small juveniles are associated with macroalgae, seagrass beds, or *Porites* clumps (Section 2.21). The depth range of the Nassau grouper (0–100 m) may be influenced more by the availability of suitable habitat than by food resources, since diet is highly varied and more a function of body size than of water depth (Section 3.41).

Since adults are known to migrate long distances to reach spawning sites (Section 3.51), proximity to these sites during non-reproductive periods is apparently not critical although the sites themselves may be essential for reproduction. It is probable that spawning sites are quite specific and that their destruction or disturbance

could negatively impact spawning activity of population(s) that utilize such sites. In this respect, species like the Nassau grouper, which may depend for their reproduction on highly specific spawning areas, could be severely habitat-restricted, the spawning sites forming significant bottlenecks in their life cycle. The loss of local stocks following the elimination of local spawning aggregations in a number of insular areas (e.g. Bermuda and Puerto Rico) suggests that some populations are partially self-recruiting, although further genetic studies are necessary to test this hypothesis (Section 1.33) (Sadovy, 1993).

In the wild, the Nassau grouper spawns over a narrow temperature range (25–26°C) which m'= limit the northern and southern extremes of reproductive populations and the timing of spawning migrations (Colin, 1992; Tucker et al., 1993; Carter et al., 1994). It is also feasible that distribution is influenced by the availability of suitable symbiotic cleaners (Section 3.53).

Epinephelus itajara Presence of mangrove areas appears to be important for juvenile jewfish. Reports of jewfish from the Lesser Antilles are particularly rare, probably due to limited mangrove habitat. Holes and caves provide important shelter for adults.

Table 2

Stages of gonadal maturation for 230 *Epinephelus striatus* collected in the Bahamas between May 1988 and October 1990 (from Sadovy and Colin,1995—Fig. 3). Bisexual fish are those in which the gonads contain both ovarian and testicular tissue and include both immature (both male and female tissue immature) and mature (in parentheses) bisexuals.

Size class (mm SL)	Bisexual	Female		Male	
		Immature	Mature	Immature	Mature
151–200	1	1			
201–250	2				
251–300	8	3			1
301–350	11	3			1
351–400	15	2			
401–450	4	1	2	1	1
451–500	9		10		23
501–550	4(1)		36		15
551–600	(3)		33		9
601–650			13		4
651–700			5		6
701–750			1		1
Total	58	10	100	1	61

3 ECONOMIC AND LIFE-HISTORY

3.1 Reproduction

3.11 Sexuality

Epinephelus striatus Like most other groupers, the Nassau was originally considered to be a monandric protogynous hermaphrodite, whereby all males derive from the sex change of adult females (Smith, 1971; Claro et al., 1990; Carter et al., 1994). Evidence of a change from adult female to adult male in the Nassau (i.e. fish undergoing sexual transformation whereby the gonads show degeneration of mature tissue of one sex and proliferation of reproductive tissue of the other), however, is weak (Sadovy and Shapiro, 1987; Shapiro, 1987). Other characteristics are also inconsistent with a diagnosis of monandric protogyny such as the strong male/female size overlap, the presence of males that develop directly from the juvenile phase, and the mating system (Section 3.16) (Colin, 1992; Sadovy and Colin, 1995). Nassau grouper pass through a juvenile bisexual phase (the gonads consist of both immature spermatogenic and immature ovarian tissue) (Table 2), and mature directly as male or female (Sadovy and Colin, 1995). Although the Nassau grouper is capable of changing sex following hormone injection—one Nassau grouper reproduced as a female and subsequently as a male approximately 6 months later, following an LHRH-a implant in captivity (Watanabe and Head[11], Watanabe et al., 1995a)—natural sex change has not been confirmed. The close affinity of this species with other hermaphroditic serranids accounts for the gonad structure of this species (Section 3.15) and although it may retain a capacity for natural sex change, available evidence indicates that this is not typical and that the Nassau grouper is primarily gonochoristic (separate sexes) (Sadovy and Colin, 1995).

Epinephelus itajara There is no conclusive evidence regarding the sexual pattern of the jewfish (Bullock et al., 1992), although protogynous hermaphroditism has been suggested due to the presence of regressive oocytes of unspecified maturation stage within the testis of a 1,602 mm SL male (Smith, 1959, 1971). Bullock and Smith (1991) and Smith (1971) examined testes with a lumen and peripheral sperm-collecting sinuses (features often found in protogynous species) but also noted a number of small (relative to females) (887 mm SL) mature males, indicating that some males mature directly as males. The evidence is insufficient to con-

[11] Watanabe, Wade, and William Head. 1992. Caribbean Marine Research Center, Vero Beach Laboratory, 805 East 46th Place, Vero Beach, FL 32963. Personal commun.

Table 3

Summary of life history parameters for Nassau grouper, *Epinephelus striatus*, and jewfish, *E. itajara*. The area and source are indicated in parentheses, where known.

	Epinephelus striatus	*Epinephelus itajara*
Age and length at maturity	5 yrs, 580 mm SL (Virgin Islands) (Olsen and LaPlace, 1979)	6-7 yrs, 1200-1350 mm TL females; 4-6 yrs, 1100-1150 mm TL males (E. Gulf of Mexico) (Bullock et al., 1992)
	420-450 mm SL females 400-450 mm SL males\4+ yrs (Cayman Islands) (Colin et al., 1987; Bush et al., in press)	
	500 mm TL (minimum size ripe males) (Cayman Islands) (Tucker et al., 1993)	
	425 mm SL females; 402 mm SL males, immatures are 3-6 yrs (otolith growth zones not validated) (Bahamas) (Sadovy and Colin, 1995)	
	483 mm TL (North Carolina-Florida) (SAFMC, text footnote 24)	
	480 mm TL (Jamaica) (Thompson and Munro, 1978)	
Age and length at first capture	< 300 mm TL & 4-5 yrs (Virgin Islands) (Olsen and LaPlace, 1979; CFMC, text footnote 26)	508 mm (Gulf of Mexico) (GMFMC, text footnote 9)
	6-7 yrs (Cayman Islands) (Bush et al., in press)	
	275-625 mm TL (mean = 570) (Jamaica) (Thompson and Munro, 1978)	
	300-500 mm TL depending on size limits (North Carolina-Florida) (SAFMC, text footnote 46)	
	450 mm TL (South Florida) (Bohnsack, 1990)	
Maximum age and length	1200 mm TL (CFMC, text footnote 26)	2400 mmTL (Virgin Islands) (CFMC, text footnote 26)
	9 yrs, 910-960 mm SL (Olsen and LaPlace, 1979) (Virgin Islands)	
	17 yrs, 710 mm TL, 6700 g (Cuba) (Claro et al., 1990)	37 yrs, 2155 mm TL females 26 yrs, 2057 mm TL males (E. Gulf of Mexico) (Bullock et al., 1992)
	755 mm SL (Bermuda) (Bardach et al., 1958)	2500 mm TL (Heemstra and Randall, 1993)
	840 mm TL (Jamaica) (Thompson and Munro, 1978)	
	640 mm TL (Netherlands Antilles) (Nagelkerken, 1981)	
	29 yrs, 850mm FL (Cayman Islands) (Bush et al., in press)	

firm hermaphroditism and discount gonochorism (Sadovy and Shapiro, 1987). Of 481 jewfish examined, none were undergoing sexual transition, males and females overlapped in size, and the sex ratio did not differ from unity.

3.12 Maturity

Epinephelus striatus Male and female Nassau grouper typically mature between 400 and 450 mm SL, with most individuals attaining sexual maturity by about 500 mm SL and 7 years (Table 3), although the smallest mature fish recorded in Cuba was a male in the 360–390 mm TL size class (Claro et al., 1990). From otolith ageing work, the minimum age at sexual maturity is between 4 and 8 years (Bush et al., in press) with most fish spawning by age 7+ years (Olsen and LaPlace, 1979; Bush et al., in press). Nassaus raised from the egg in captivity matured at 27–28 months (400–450 mm SL) (Tucker and Woodward, 1994). Thus size, rather than age, may be the major determinant of sexual maturation.

Epinephelus itajara Sexual maturity in jewfish from the eastern Gulf of Mexico was determined histologically (Bullock et al., 1992) (Table 3). Males matured at a smaller size and somewhat younger age than females. Males <1,150 mm TL were immature with 50% mature by 5–6 years. All males larger than 1,155 mm TL and older than 7 years were mature. Female jewfish first mature at 1,200–1,350 mm TL and 6–7 years; all females larger than 1,225 mm TL and older than 6 years were mature (Bullock et al., 1992).

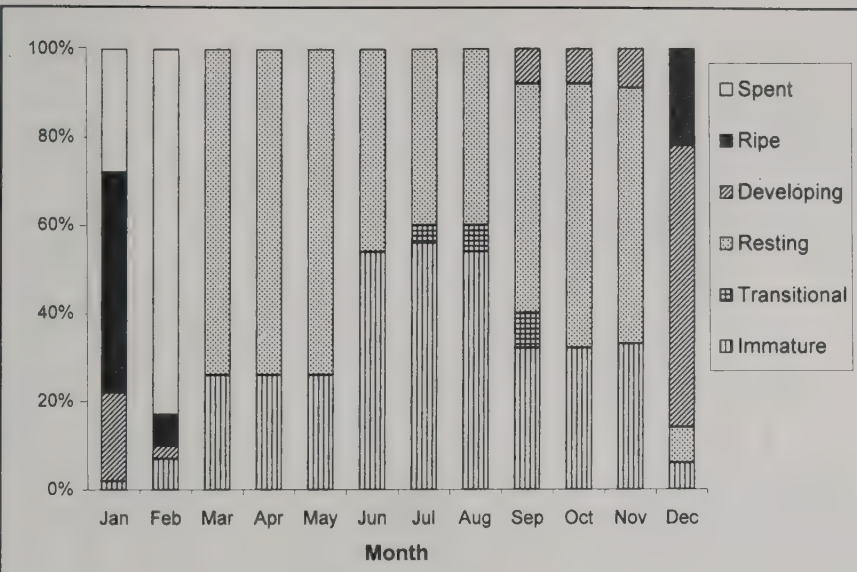

Figure 7
Monthly distribution of percent frequency of different gonad development stages for female Nassau grouper, *Epinephelus striatus*, collected from Belize from 1984–86 (n=1,232) (redrafted from Carter et al., 1994).

3.13 Mating

Epinephelus striatus The reproductive season in the Nassau grouper is brief and evidently associated with temperature and moon phase, according to GSI, gonadal histology, macroscopic, and oocyte diameter analyses. At lower latitudes, reproductive activity lasts for about one week per month, for one to three months each year, between December and February (Fig. 7), either peaking in January (Smith, 1972; Olsen and LaPlace, 1979; Claro et al., 1990; Colin, 1992; Powell and Tucker, 1992; Aguilar-Perera, 1994; Miller[12]) or between January and April (Thompson and Munro, 1978). In more northerly latitudes (i.e. Bermuda and Florida), the reproductive season falls between May and August, peaking in July (Oliver La Gorce, 1939; Smith, 1971; Burnett-Herkes, 1975). Exceptions to the possible latitudinal pattern were the capture of recently spawned females in September in Cuba and the observation, in the same month, of a school of Nassau grouper at 29 m depth exhibiting probable spawning behavior in this location (Claro et al., 1990).

All spawning, as far as is known, occurs in distinct aggregations. Neither aggregation nor spawning have been reported from South America although ripe Nassaus are frequently taken (Cervigón[13]). Aggregation spawning is likewise unknown from the Lesser Antilles, from Central America south of Honduras, or from Florida, despite commercial landings in many of these areas. Whether these reports indicate a different spawning strategy, or loss of aggregations that once formed, is not known.

Spawning in the wild is highly synchronized and occurs briefly within about a week of full, or between full and new, moon (Smith, 1971; Colin, 1992; Tucker et al., 1993; Aguilar-Perera, 1994; Carter et al., 1994; Tucker and Woodward, 1994; Department of Fisheries, Government of the Bahamas), within the narrow temperature range of 25–26°C and over a wide range of daylengths (Colin, 1992; Tucker et al., 1993; Carter et al., 1994) (see also Section 7). Similar associations between reproduction, temperature, and lunar phase were also noted in captive animals. Nassau grouper raised from egg to maturity in Florida and Bermuda under conditions of ambient light, temperature, and salinity, exhibited ovarian maturation, ovulation, behavior, and color changes characteristic of spawning, at 26°C, although no spawning was observed (Tucker and Woodward, 1994). Temperature is evidently a more important stimulus for spawning than day length, according to patterns of voluntary spawning in captive fish; while spawning occurred at temperatures ranging from

[12] Miller, W. 1984. Spawning aggregations of the Nassau grouper, *Epinephelus striatus*, and associated fishery in Belize. Advances in Reef Sciences, October 26–28, 1984, University of Miami, Florida. Unpubl. data, p. 19.

[13] Cervigón, Fernando. 1991. Fundacion Cientifica Los Roques, Aptdo. 1139, Caracas 1010A, Venezuela. Personal commun.

23.1–27.9°C, 24–27°C was the most suitable based on spawning frequency and volume, and egg and larval development (Tucker, 1994; Watanabe et al., 1995b; Tucker et al., 1996). Nassau grouper spawned spontaneously one day prior to the new moon in April 1963 in an aquarium in Cuba under artificial light and water temperature of 24.9°C (Guitart-Manday and Juárez-Fernandez, 1966).

Epinephelus itajara The reproductive season of the jewfish occurs between June and October but, as for the Nassau grouper, varies with geographic location. Jewfish in the eastern Gulf of Mexico have ripe gonads from June through September, with peak activity indicated from July through September (Bullock et al., 1992) (Figs. 8A and B). Presumed courtship activity was observed in small groups (8–12) of jewfish off southwestern Florida in August and September around the time of the full moon, although no spawning was observed (Colin, 1994). Jewfish (known locally as the "June Fish") in Belize spawned inshore in creeks, estuaries, and lagoons in July and August. In Puerto Rico, ripe individuals appeared in July and August (Erdman, 1976). In Colombia, the main spawning season is believed to be in September and October (Carlos A. Bohorquez cited in Colin, 1989).

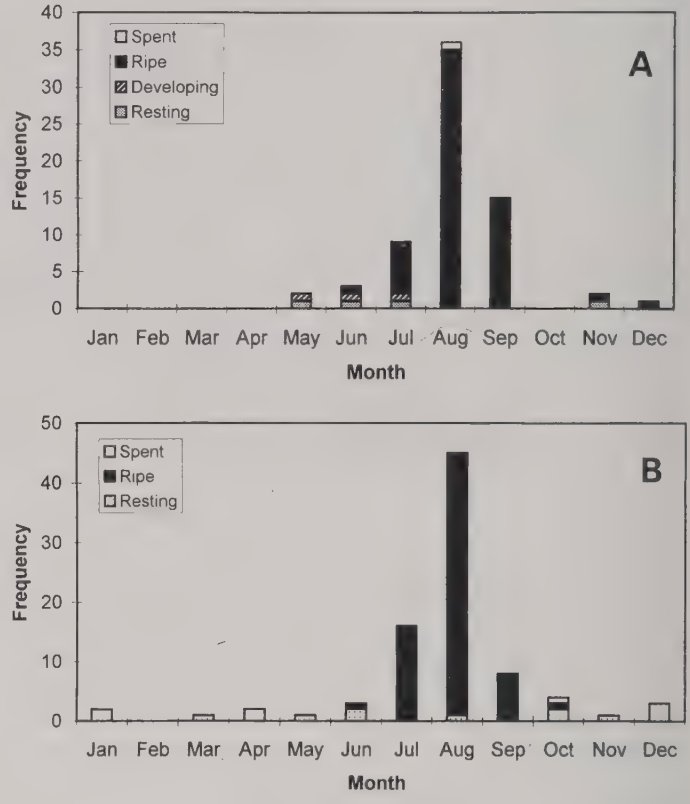

Figure 8
Monthly distribution of gonad classes for mature (A) female (n=86) and (B) male (n=66) jewfish, *Epinephelus itajara*, collected from the eastern Gulf of Mexico (redrafted from Bullock et al., 1992)

3.14 Fertilization

Epinephelus striatus See Section 3.21.

Epinephelus itajara No information available.

3.15 Gonads

Epinephelus striatus As in other epinepheline serranids, Nassau gonads consist of a bilobate, hollow sac lying below and posterior to the air bladder and connected to it by mesenteries (Smith, 1965). The lobes of the ovary are unequal in size and fused posteriorly with the lumina forming a common oviduct which descends to the genital region immediately behind the anus. The urinary bladder and its duct are closely bound to the posterior face of the common oviduct. There is no germinal epithelium in the common oviduct and the wall of the gonad is composed of smooth muscle and connective tissue (Smith, 1965; Carter et al., 1994). Possible endocrine tissue masses of the type described in other serranids (e.g. Lavenda, 1949; Smith, 1965) are visible close to the main vein and artery in juveniles and adults (Sadovy and Colin, 1995). All ovaries and testes have a lumen with an alamellar region located laterally in juveniles and ventrally in adult males and females (Carter et al., 1994; Sadovy and Colin, 1995). The testicular organization is of the "unrestricted spermatogonial testis-type" (Grier, 1981).

Gonadosomatic indices (GSI), calculated for ripe testes and ovaries, are similar for males and females with a maximum GSI of 19% for a hydrated female and 16% for ripe males (Tucker et al., 1993; Carter et al., 1994; Sadovy and Colin, 1995). The high male GSIs of the Nassau grouper are noteworthy in that they are uncharacteristic of grouper species wherein ripe male GSIs are typically low compared to those of ripe females (Sadovy et al., 1994). The high GSI of ripe Nassau males is indicative of sperm competition (e.g. Choat and Robert-

son, 1975) among males that spawn in small groups, one female to several males; this mode of spawning has not been described in any other grouper (Section 3.16). Ripe females can be identified by a distended abdomen and a characteristic bulge between the anus and the urinary papilla (Tucker et al., 1991).

Epinephelus itajara The ovaries of jewfish have not been described. Testes exhibit a lumen and peripheral sperm sinuses and contain remnants of many ova (Smith, 1959, 1971; Bullock and Smith, 1991). Few data are available on GSI of jewfish since specimens have often been gutted by the time they are examined. Four males, ranging in length from 1,610–1,935 mm TL (92.3–155.5 kg), had ripe testes weighing from 0.68–2.00 kg and GSIs of 0.59–1.46%, while the largest ovary weighed was 16.36 kg (Bullock[14]).

3.16 Aggregation and spawning

Epinephelus striatus The Nassau grouper aggregates in large numbers to spawn each year. As far as is known, all reproductive activity occurs in these aggregations that form consistently at specific sites (= grouper "holes") and times. Aggregations consist of hundreds, thousands, or even tens of thousands of individuals and have persisted at known locations for periods of 50 years or more (Smith, 1972; Olsen and LaPlace, 1979; Colin et al., 1987; Fine, 1990, 1992; Colin, 1992; Carter et al., 1994; Sadovy, 1997; Claro[15]) (see also Section 5.43).

Aggregations form at depths of 6–50 m (Section 2.21), as a column or cone of fish of different color phases rising to within 17 m of the water surface (Olsen and LaPlace, 1979; Carter, 1986; Aguilar-Perera and Aguilar-Dávila, 1996). Prior to spawning, individuals mill around over the substrate exhibiting one of four distinctive color phases: (1) barred (normal) (Fig. 9A); (2) bicolor (Fig. 9B); (3) white belly (Fig. 9C); or (4) dark phase (Fig. 9D). There are intergradations of these patterns, with rapid changes among patterns possible (Colin, 1992). The barred color phase is found among fish in the aggregation in the morning. The bicolor phase, first described by Smith (1972), occurs in both males and females and is dominant during the late afternoon with most fish becoming bicolored by dusk, when spawning occurs (Colin, 1992). In this phase, the upper body and head become dark while the belly, lower sides, lips, and all fins but the dorsal are white. A white eyebar is prominent on the head (Colin,

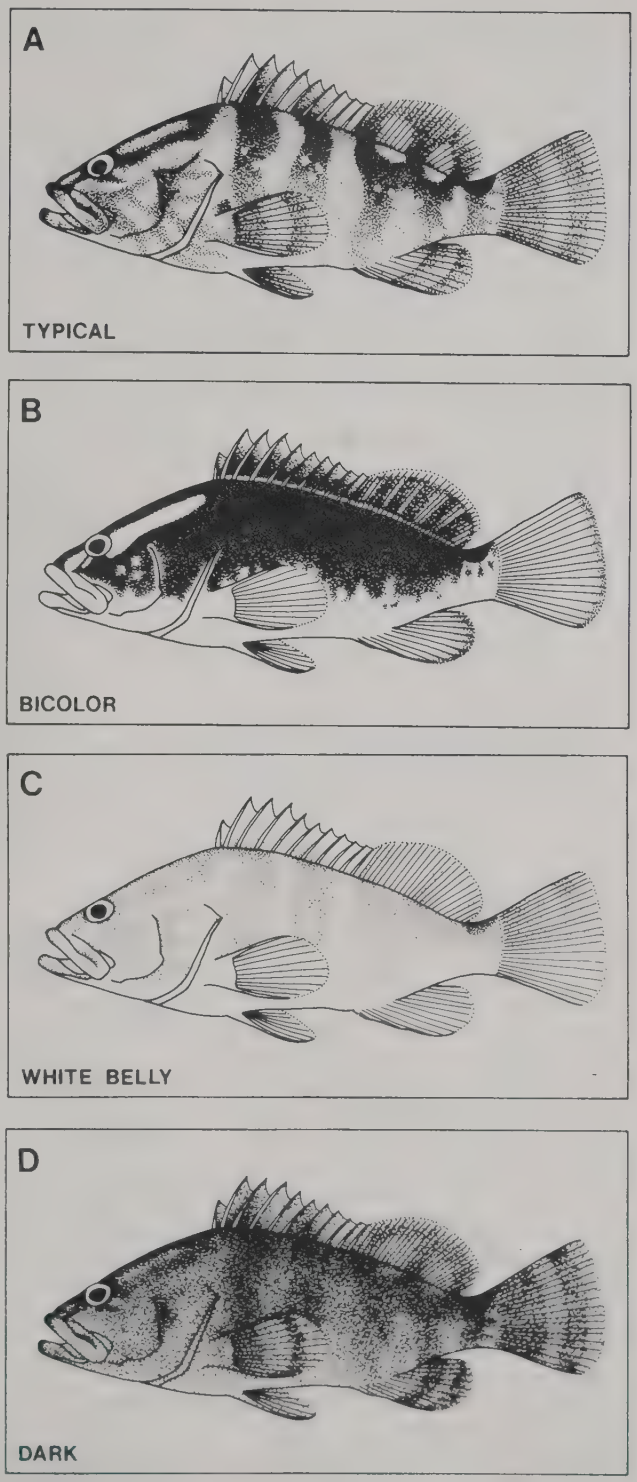

Figure 9
Color phases exhibited by the Nassau grouper, *Epinephelus striatus*: (A) typical barred coloration; (B) bicolor phase; (C) white belly phase; (D) dark phase.

[14] Bullock, Lew. Florida Marine Research Institute, 100 8th Avenue, SE, St. Petersburg, FL 33701. Unpubl. data, 13 p.
[15] Claro, Rodolfo. 1991. Laboratory of Fish Ecology, Institute of Oceanology, #18406 Playa, Havana, Cuba. Personal commun.

1992). In the white belly phase, seen among presumed females with bulging abdomens (probably full of ova), the normal color pattern is modified such that the abdominal area is distinctly white (Colin, 1992). The last pattern, the "dark" phase, is found in courting and spawning fish; the body and fins become dark gray to black with the barred pattern visible beneath the dark pigmentation. These fish are probably females ready to spawn since they appear to lead group-spawning events (see below) (Colin, 1992).

Courtship is indicated by two behaviors which occur late in the afternoon: "following" and "circling" (Colin, 1992): "following" occurs as one or more fish in the bicolor phase swim closely behind an apparent female; "circling" occurs as a bicolor phase fish circles a barred or dark phase fish. Progression from courtship to spawning may depend on aggregation size but generally occurs as follows. Towards the late afternoon fish move progressively higher in the water column, with an increasing number exhibiting the bicolor phase (Colin, 1992; Carter et al., 1994). The aggregation then moves into deeper water shortly before spawning (Colin, 1992; Tucker et al., 1993; Carter et al., 1994) by which time all individuals are either "dark phase" or "bicolor". Bicolor fish then follow dark phase fish closely and group-spawning occurs in sub-groups of 3–25 fish, apparently led by a "dark phase" fish followed by a varying number of bicolor fish. Smaller aggregations tend to include fewer bicolor phase fish and general activity and color changes are less intense (Colin, 1992; Aguilar-Perera and Aguilar-Dávila, 1996).

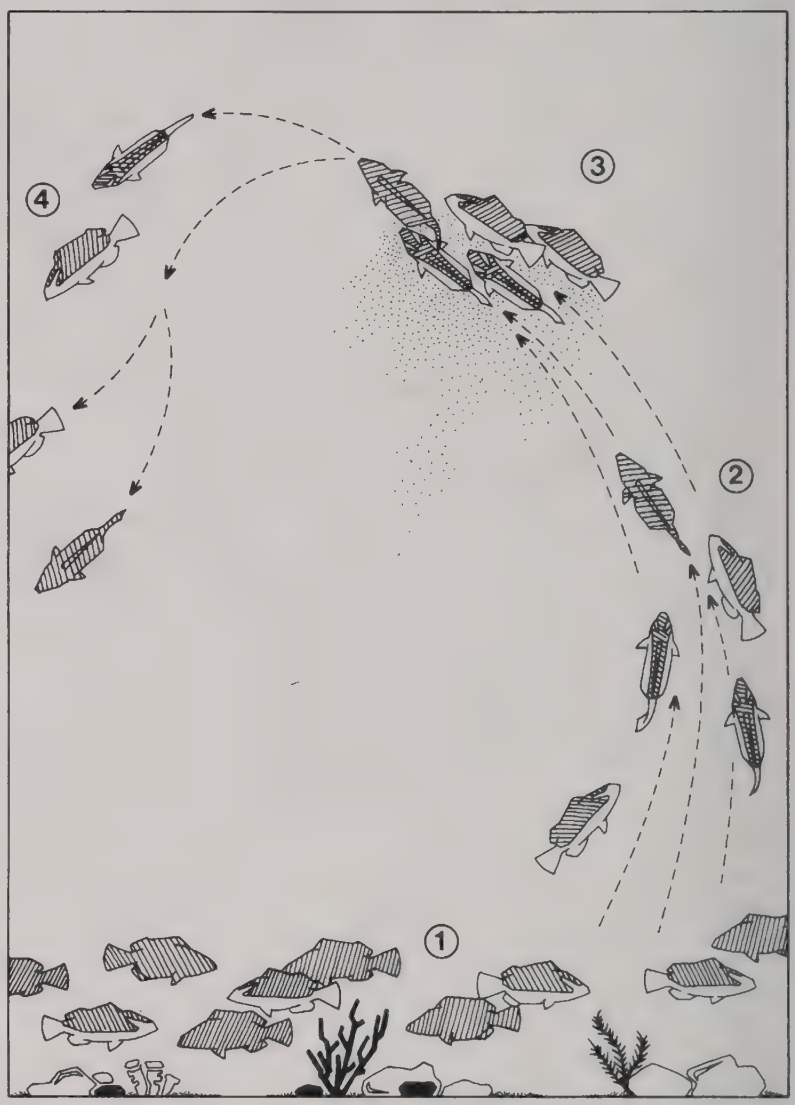

Figure 10

Spawning behavior in the Nassau grouper, *Epinephelus striatus*: (1) fish start to move up into the water column and an increasing number take on the bicolor phase; (2) ascent by a small sub-group led by a dark-phase individual followed by bicolors; (3) release of sperm and eggs; (4) rapid return of fragmented sub-group to the substrate (description from Colin, 1992); figure reproduced from Sadovy (1996), with permission from Chapman & Hall Publishers.

Spawning involves a rapid horizontal swim followed by a circling ascent of small sub-groups into the water column, with release of sperm and eggs and a rapid return of the fragmented sub-group to the substrate (Fig. 10). On the basis of observations of over 50 spawning events, the earliest and latest spawnings occurred within 20 minutes of sunset and most within 10 minutes of sunset (Colin, 1992) (Fig. 11). Hydration of vitellogenic eggs occurs in the afternoon shortly before spawning (Fig. 12).

Although aggregations form more than once at a particular site during a reproductive season, it is unclear whether the same individuals participate each time. However, several females from one aggregation contained ripe and sub-ripe oocytes together with post-ovu-

latory follicles (which remain after mature oocytes have been released), suggesting that individual females spawn repeatedly on different days during one aggregation (Smith, 1972; Sadovy, personal observ.). Moreover, examination of spawning on videotape indicated that during 3–4 successive gamete releases by a sub-group within a 15–20 second period, the same female led all spawning events, again indicating multiple egg releases in one evening (Colin, 1992). No data are available, however, addressing whether each mature female spawns in every aggregation month, or indeed, each year (but see Section 3.51).

It is not known how Nassau grouper select and locate aggregation sites or why they aggregate to spawn. To locate a site, this species could swim up- or down-current along the shelf break to reach the most seaward upcurrent extension of the reef where aggregation sites are generally located (Carter, 1986; Colin et al., 1987) (Section 2.21). The timing and synchronization of spawning may be determined by the necessity for widely dispersed adults to coordinate their reproductive activities, may facilitate egg dispersal, or minimize predation on adults or eggs (Colin, 1992).

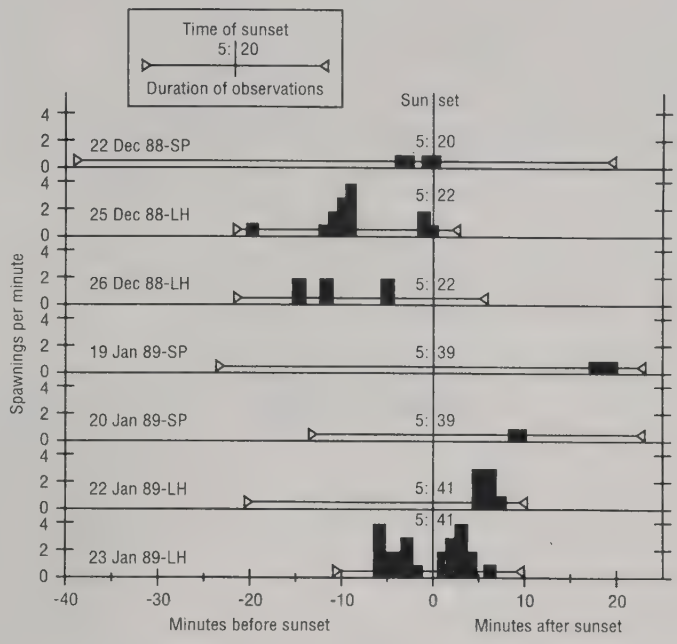

Figure 11

Frequency and timing of spawning by the Nassau grouper, *Epinephelus striatus*, at two aggregation sites (SP=South Point; LH=Little Harbor) off Long Island, Bahamas. The horizontal line indicates the observation period and all lines are adjusted so that sunset occurs at the same relative time (from Colin, 1992).

Prior to spawning, fish migrate toward aggregation sites in groups numbering between 25 and 500, moving parallel to the coast or along the shelf edge (Colin, 1992; Carter et al., 1994; Aguilar-Perera and Aguilar-Dávila, 1996). "Corridas de desove" (spawning runs), which refer both to the migration of fish toward a spawning site and to the aggregation itself, were first described in Nassau grouper from Cuba in 1884 by Vilaro Diaz, and later by Guitart-Manday and Juárez-Fernandez (1966). All three workers noted that fishers reported "corridas" occurring mainly between November and February and at different moon phases. It is not known whether "corridas" are exclusively associated with spawning or occur at other times, unassociated with reproductive activity.

Epinephelus itajara Jewfish appear to aggregate in greater numbers when reproductively active than in non-reproductive periods and are therefore believed to aggregate to spawn. Aggregation sites are known only from Belize, southeast and southwest Florida (Atlantic and Gulf of Mexico waters), and Colombia (Fig. 6). An aggregation at English Cay, southeast of Belize City, Belize, consisted of 50–60 individuals and formed sometime between June and October (Domeier and Colin, 1997; Auil[16]). Females at these aggregations had advanced vitellogenic oocytes and males contained running milt indicating recent or imminent spawning. In Colombia, jewfish aggregate in September and October (Carlos A. Bohorquez cited in Colin, 1989). In southwest Florida, they aggregate in August and September on shipwrecks in 30–45 m of water (Eklund, personal observ.).

Aggregations during the reproductive season typically number from a few fish to more than 100 individuals, although many have declined in fish number in recent years (see also Section 4.2). About 20–30 large jewfish (45–200 kg) were reported in June 1971 at a wreck at 36 m depth off southwest Florida (Smith, 1976) and adults have also been observed by divers on offshore wrecks at depths of 36–46 m (Bullock and Smith, 1991). At aggregation sites off southwest Florida (30–40 m depth) number of fish declined from 25–150 in 1982–83, to 0–5 in 1989 (DeMaria[17]),

[16] Auil, Stephanie. 1991. University of the West Indies, P.O. Box 863, Belize City, Belize. Personal commun.

[17] DeMaria, Don. 1990. P.O. Box 420975, Summerland Key, FL 33042 Personal commun.

increasing again following the moratorium on capture; 13 sites have been noted (Koenig et al.[18]).

Details of behavior are known from southwest Florida aggregation sites. Colin (1994) observed 8–12 large jewfish (60–150 kg) at 33 m depth on a wreck. Two of the fish were present for both August and September observations. Courtship was most common from late morning to mid-afternoon. Presumed males (sexes could not be verified but were assigned on the basis of color and behavior) exhibited a pale head and dark body coloration when courting (Colin, 1994), while presumed females did not change color during courtship. Courtship consisted of a male nuzzling the vent area of females and of males and females rising and turning together in the water column. Loud, low frequency sounds (booms) were emitted, possibly related to courtship and territorial defense (Colin, 1994). Intense interactions, including vent nuzzling, between fish have been observed when they are "stacked" in layers off the bottom in a well-defined mass (Koenig et al.[18]).

[18] Koenig, C., F. Coleman, and A. M. Eklund. 1997. Studies of the jewfish (*Epinephelus itajara*) in the eastern Gulf of Mexico. Unpubl. report to The Curtis and Edith Munson Foundation, 26 p.

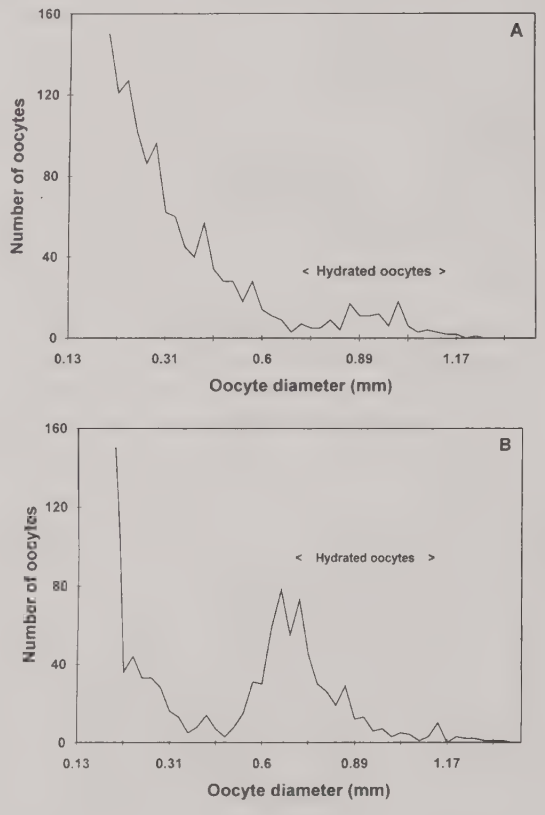

Figure 12
Oocyte diameter frequencies taken in (A) the morning (SL=508 mm) and (B) the afternoon (SL=551 mm) of 22 December 1988 during the spawning season of the Nassau grouper, *Epinephelus striatus*, from the Bahamas from two reproductively active females. Vitellogenic oocyte diameters range from 0.17-0.71 mm and hydrated oocytes are greater than 0.71 mm. [Figure prepared by Pat Colin, Yvonne Sadovy, and George Mitcheson as part of a project supported by the Caribbean Marine Research Center, National Undersea Research Program, NOAA; P. Colin - project leader.]

3.17 Spawn

Epinephelus striatus Fertilized eggs are pelagic, measure about 1 mm in diameter, and have a single oil droplet of 0.22 mm diameter (Guitart-Manday and Juárez-Fernandez, 1966). Artificially fertilized eggs are neutrally (at 32‰) or positively buoyant and measure 0.9 to just over 1 mm in diameter, with a single oil globule averaging 0.24 mm (Colin, 1992; Powell and Tucker, 1992). Following voluntary spawning under artificial conditions, sperm were collected and described as having a "piriform" cephalic portion and an extraordinarily long tail (Guitart-Manday and Juárez-Fernandez, 1966).

Epinephelus itajara No information.

3.2 Preadult phase

3.21 Embryonic phase

Epinephelus striatus Eggs hatch 23 to 40 hours following fertilization. Embryonic development of eggs produced in a Havana aquarium was followed from fertilization to absorption of the yolk sac at 2.8 mm TL (72 hours); eggs hatched in about 40 hours at 25°C (Guitart-Manday and Juárez-Fernandez, 1966). Artificially fertilized eggs hatched within 27–29 hours of fertilization at 25°C, 23–25 hours at 28°C (Powell and Tucker, 1992), and 24 hours in ambient water temperature (Colin, 1992).

Epinephelus itajara No information.

3.22 Larval and juvenile phases

Epinephelus striatus Larval and early juvenile phases are well described for the Nassau grouper. Newly hatched larvae from induced spawnings measured 1.7–1.8 mm notochord length (NL) (Powell and Tucker, 1992). Larvae had pigmented eyes 48 hours post-hatching and began feeding within 60 hours (Tucker et al., 1991). Development is described for laboratory-reared specimens from the egg to a 13.5 mm SL larva approximately 40 days post-hatching (Powell and Tucker, 1992) (Figs. 13A–13G). Fins

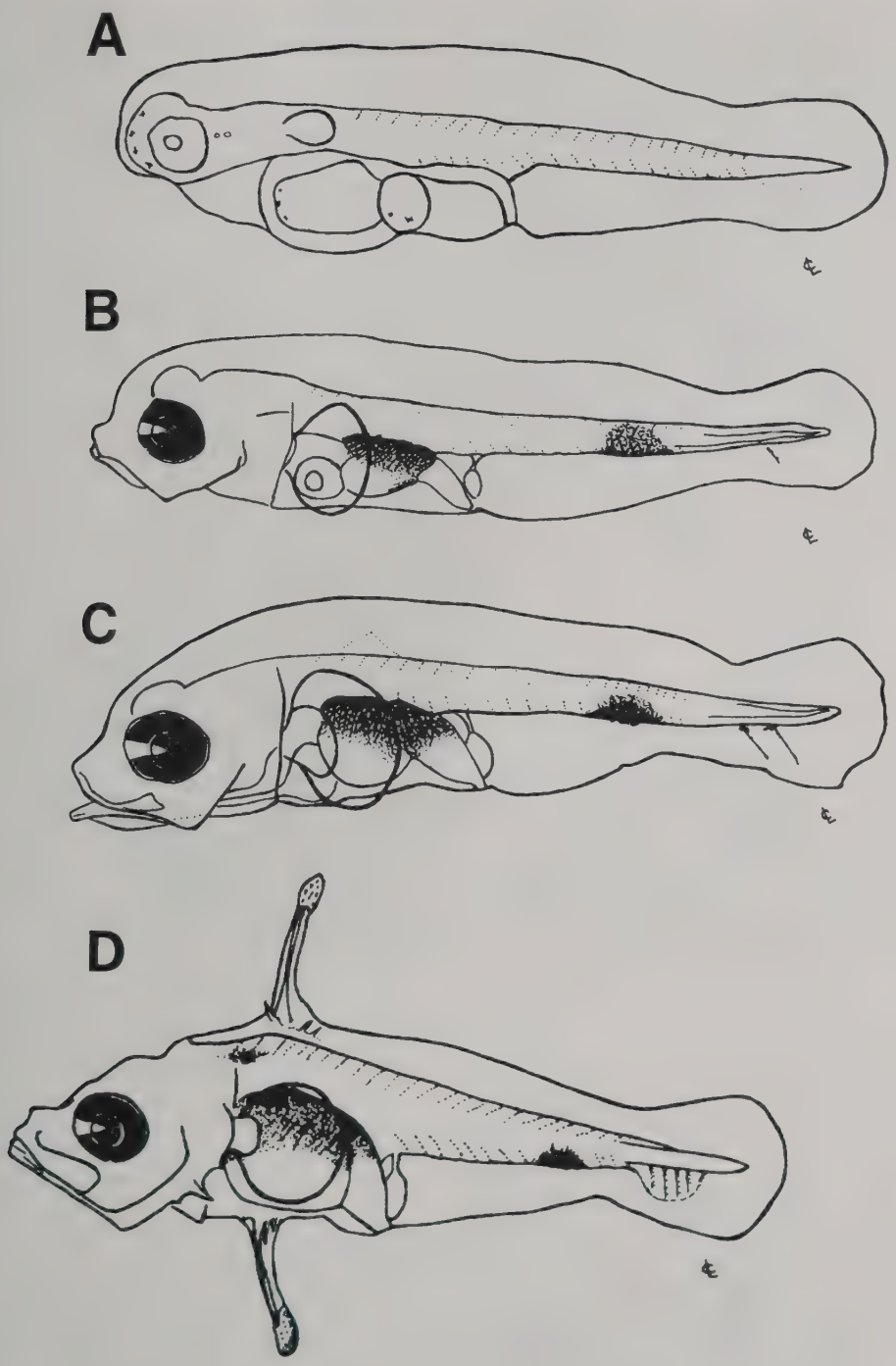

Figure 13

Developmental stages of laboratory-reared Nassau grouper, *Epinephelus striatus*: (A) 2.5 mm NL early yolk-sac larva, 1 day old; (B) 2.6 mm NL late yolk-sac larva, 3 days old; (C) 2.9 mm NL preflexion larva, 5 days old; (D) 4.9 mm NL early flexion larva, 13 days old. On facing page: (E) 6.2 mm NL late flexion larva, 20 days old; (F) 6.8 mm SL postflexion larva, 25 days old; (G) postflexion larva, 13.5 mm SL, 40 days old (with permission from Powell and Tucker, 1992).

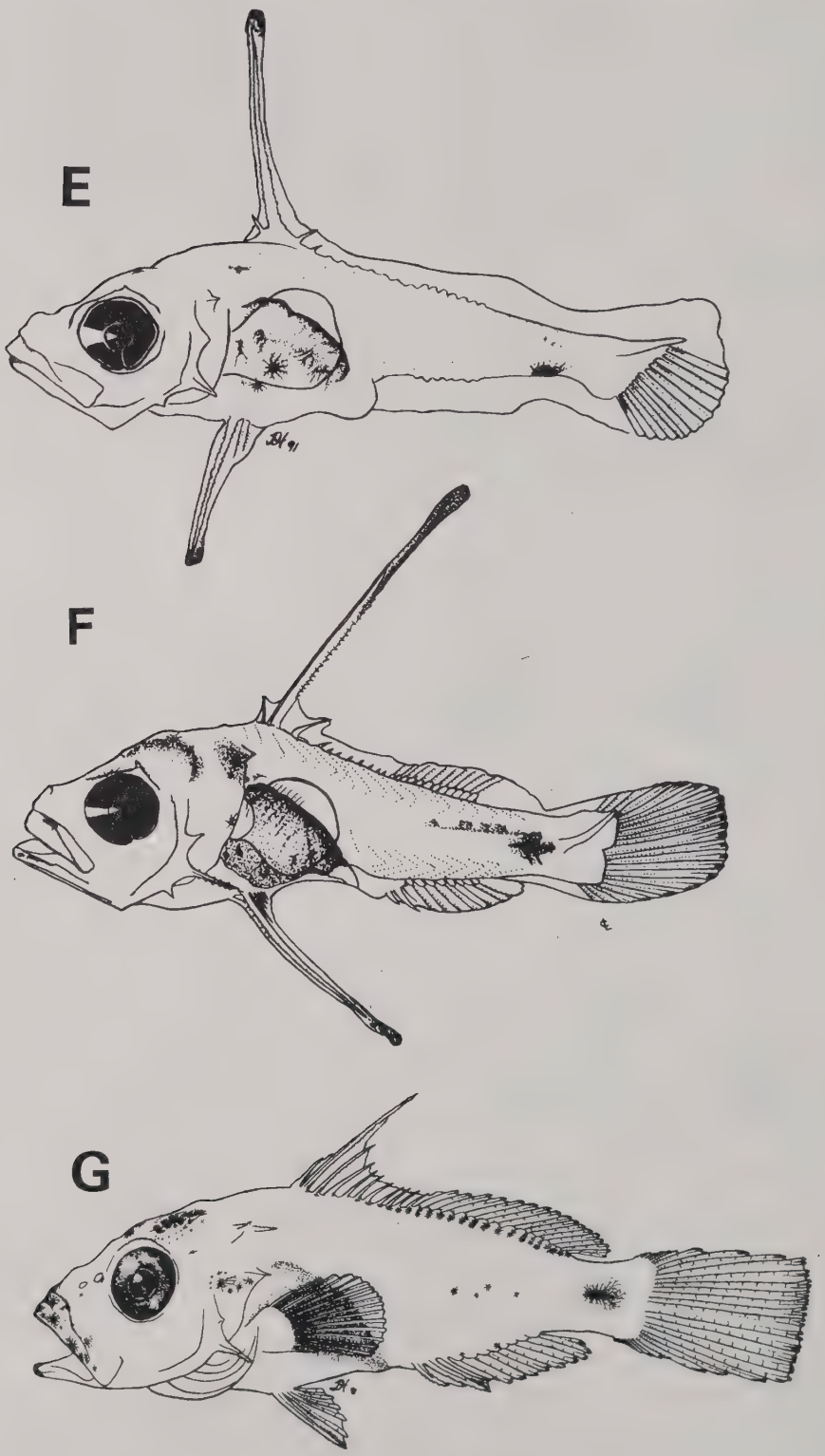

Figure 13 (continued)

develop in the order of pelvic, first dorsal, caudal, pectoral, anal, and second dorsal. The adult complement of principal caudal fin rays was attained at 6.0 mm SL and of dorsal spines at the postflexion stage at approximately 6.6 mm SL with completion of first and second dorsal and anal fins at 7.4 mm SL. Preflexion larvae become flexion larvae over the range of 5.0–5.4 mm NL and flexion to postflexion occurs between 6.0 and 6.5 mm NL (Powell and Tucker, 1992). Larvae were planktonic until 42–70 days post-hatching with transformation occurring in less than one week (Powell and Tucker, 1992; Tucker and Woodward, 1994).

Newly hatched larvae are inconspicuously pigmented and slightly curved around the yolk sac when artificially reared (Powell and Tucker, 1992). Wild-caught larvae exhibit several small, dendritic melanophores on the snout (Smith, 1971; Laroche[19]) (Fig. 14A). Yolk-sac larvae with a developing mouth have a characteristic pigment pattern in the form of a distinct "inverted saddle" on the ventral midline and lateral surface of the caudal peduncle (Figs. 13A–G) (Powell and Tucker, 1992) and specimens <21 mm SL also lack the caudal peduncle blotch which is found in all fish >35 mm (Smith, 1971). Pigment patterns change markedly during the flexion stage, and young postflexion larvae (<6.8 mm SL) are similar to late flexion larvae. In small juveniles there is a characteristic line of black spots along the bases of the dorsal rays posterior to the fifth spine (Smith, 1961) (Figs. 13G and 14B). The pattern of vertical bars seems to develop at about 40 mm in specimens from the Bahamas (Smith, 1961).

It is highly unlikely that preflexion and flexion epinepheline larvae can be positively identified as *Epinephelus striatus* until a comparative study of epinepheline larvae is made, although certain combinations of pigment, fin spinelets, and spine lengths narrow down possibilities (Kendall, 1979; Johnson and Keener, 1984; Powell and Tucker, 1992). With postflexion larvae greater than 7.4 mm SL it is possible to separate Nassau grouper from other groupers, except for *E. adscensionis*, on the basis of dorsal and anal fin ray counts, spinelet configuration, second first-dorsal-fin spine length relative to SL, and capture location (Powell and Tucker, 1992).

Larvae attain a maximum size of 30 mm SL (average 23.4 mm) by 36 days after presumptive spawning (Shenker et al., 1993). Larvae collected 10 days after probable spawning measured 6–10 mm SL. Over a 15-day period, 8–22 days after the full moon, larval sizes increased from 5.7 to 10 mm SL (Greenwood, 1991; Shenker et al., 1993). Pelagic juveniles were collected up to 46 days following a presumptive spawning moon, and benthic juveniles were first found on artificial and natural reefs at 47 days. Pelagic juveniles taken in channel nets just prior to settlement measured 22–27 mm SL (Colin, 1992; Colin et al., 1997) (Fig. 14C). Transition from larval to juvenile phases occurs at 6–7 weeks for wild fish and 6–10 weeks for fish raised under artificial conditions from induced spawns. The wild-caught larvae grew more slowly than larvae from induced spawns (Shenker et al., 1993; Tucker and Woodward, 1994; Colin et al., 1997).

Presumptive daily increments in lapilli of wild-caught larvae indicate a larval period of 35–40 days and support fertilization at the full moon. A mean larval period of 41.6 days was indicated from net-caught samples (Fig. 15) (Colin, 1992; Colin et al., 1997). Presettlement otolith increments were distinct and easily counted, however, settlement marks were not as apparent. It was assumed that the first otolith increment forms after yolk absorption, at least 4 days post-fertilization and three days post-hatch, since larvae reared in aquaria up to the stage of yolk sac absorption showed no evidence of increment formation (Colin et al., 1997).

Epinephelus itajara Little work has been done on jewfish larvae and none on the earliest stages. Larvae 6.2–17.4 mm SL were examined and dorsal and pelvic spines described in Johnson and Keener (1984). Larvae are characterized by distinctive spinelet patterns on pelvic and second dorsal spines and by a pigment spot at the cleithral symphysis, found elsewhere only in *E. cruentatus* and *Mycteroperca* spp. (Johnson and Keener, 1984). Postflexion larvae captured around mangroves in southwestern Puerto Rico in September measured 14.7–17.9 mm SL, supporting the summer spawning period in that area (Dennis et al., 1991) indicated by Erdman (1976).

3.3 Adult phase

3.31 Longevity

Epinephelus striatus The maximum age recorded for Nassau grouper is 29 years, using sagittal otoliths from the Cayman Islands (Bush et al., 1996; Bush et al., in press) (Section 3.43) (Table 3). Using length-frequency analysis, which tends to exclude younger animals, a theoretical maximum age at 95% asymptotic size is 16 years. Other maximum age estimates include individuals of up to 9 years in the heavily exploited Virgin Islands fishery (Olsen and LaPlace, 1979), 12 years in northern Cuba, 17 years in southern Cuba (Claro et al., 1990), and 21 years from the Bahamas, assuming that rings are formed annually (Sadovy and Colin, 1995). These differences in maximum age estimates are probably due, in part, to methodological differences and, in part, to the effects of local fishing pressure. Individuals of more than 12 years of age are not common in fisheries, with more heavily fished areas

[19] Laroche, Wayne. Stonefish Environmental and Taxonomic Services, Box 216, Enosburg Falls, VT 05450. Unpubl. data.

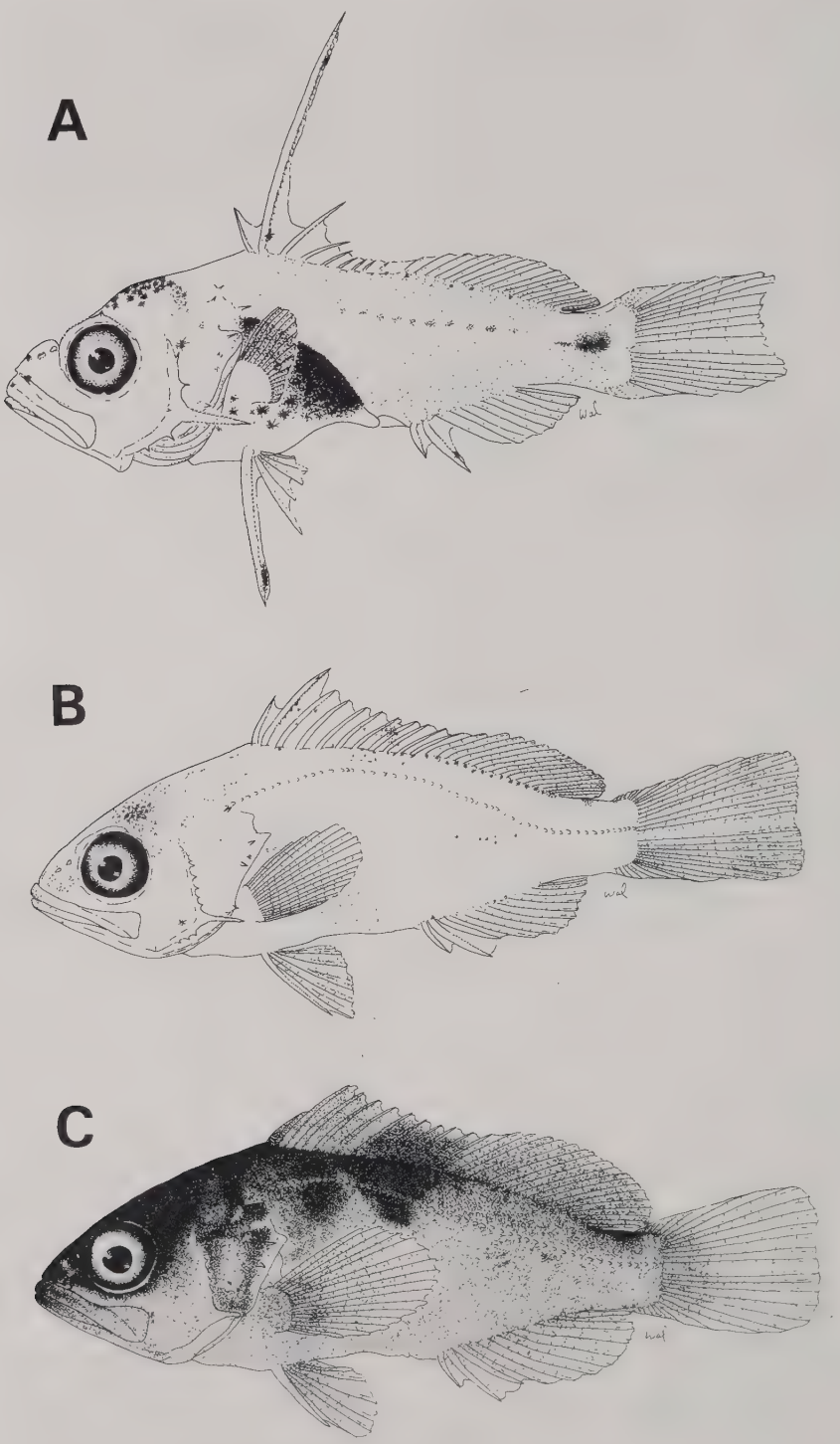

Figure 14

Developmental stages of wild-caught Nassau grouper, *Epinephelus striatus* taken in the Bahamas: (A) 9.1 mm SL taken 19 Jan 1991, tip of second dorsal spine slightly damaged; (B) 22 mm SL taken 3 Feb 1989; (C) 25 mm SL taken 2 Feb 1989 (Laroche[19]).

yielding much younger fish on average. Generation time (the average age of parents in the population) is estimated as 9–10 years based on average fish size from an unexploited aggregaton in Belize (see Section 4.13), the growth curve from the Cayman Islands (Fig. 16), and the SL-TL conversion curve from Sadovy and Colin (1995).

Epinephelus itajara Maximum ages recorded for an exploited population of jewfish males and females, based on sagittal otoliths, are 26 and 37 years respectively (Table 3). Age range for 382 jewfish taken from the eastern Gulf of Mexico was 3–26 years (n=41) for males, 0–37 for females (n=85), and 0–36 for fish of undetermined sex (n=256) (Bullock et al., 1992). Insufficient information is available to estimate generation time.

3.32 Hardiness

Epinephelus striatus Under natural conditions the Nassau grouper appears to prefer clear waters (Section 2.1) but is fairly tolerant of a range of water qualities: one adult survived for more than seven years in the old New York Aquarium in which the water at times became nearly fresh and was frequently quite polluted (Townsend, 1905).

Nassaus are considered to be hardy and able to withstand handling and manipulation (e.g. Jordan, 1917). One 8.6 kg female lay on a dry boat deck in the sun for more than two hours before receiving an HCG injection and ovulating (Tucker et al., 1991). Both male and female brooders withstood handling during induced spawning (Watanabe et al., 1995a). Several naive individuals, raised from the egg under artificial conditions, survived at least 200 days when released onto reefs at 31 months of age (Roberts et al., 1995).

Epinephelus itajara The jewfish is one of few groupers able to live in brackish water. Small jewfish have been taken in poorly oxygenated upland canals in the Tampa Bay area (Lindall et al., 1975) but the species is apparently vulnerable to stresses caused by cold water (Gilmore et al., 1978) or red tide; Smith (1976) recorded that populations of jewfish were much reduced during a 1971 red tide and that dead individuals over 45 kg were often observed.

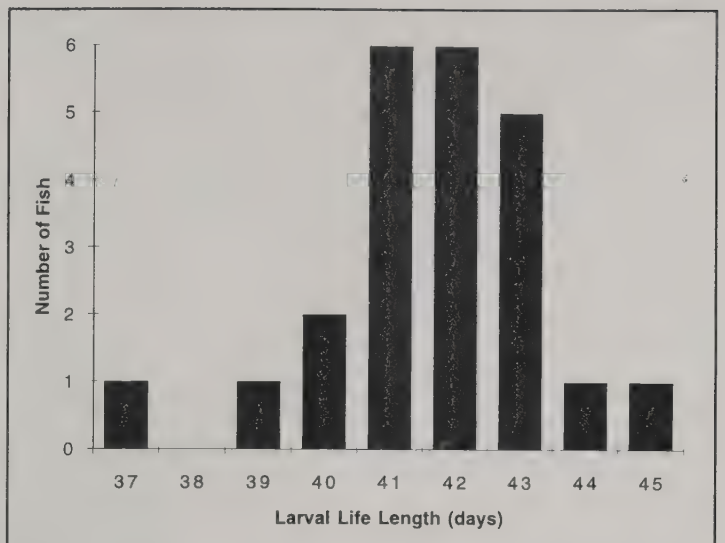

Figure 15
Pelagic life lengths (days) of the Nassau grouper, *Epinephelus striatus*, determined from pelagic and benthic juveniles captured in the vicinity of Lee Stocking Island, Exumas, Bahamas, 1989 and 1990. Pelagic life lengths were calculated from the number of pre-settlement otolith increments in lapilli plus 4 days (approximate time between spawning and first increment formation) (Colin et al., 1997, with permission).

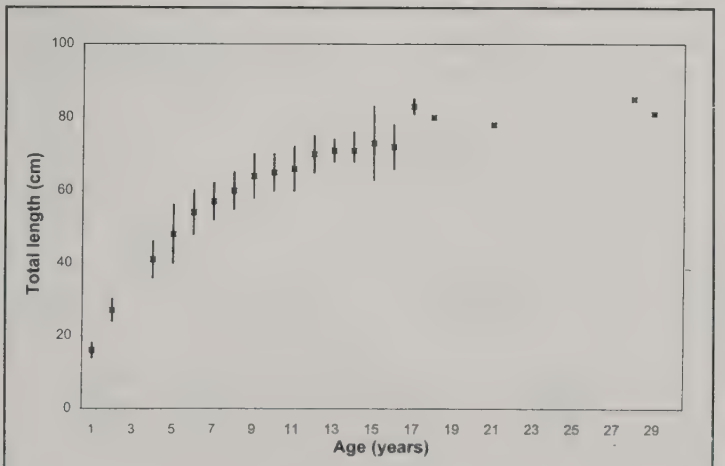

Figure 16
Observed ages (years) and total lengths (cm) for Nassau grouper, *Epinephelus striatus*, aged using sagittal otoliths, from five Cayman Island spawning aggregations (n=479), 1987–92 (Bush et al., in press).

3.33 Competitors

Epinephelus striatus Little is published on either intra- or inter-specific competition in Nassau grouper. Juve-

niles exhibit aggression towards similar-sized conspecifics and display interspecific aggression (Dunham[20]). When two non-reproductive adults, or an adult and large juvenile, encounter one another, the smaller fish acquires the bicolor pattern (Fig. 9B) described for aggregating fish (Section 3.16) in apparent submission, then turns laterally and usually swims away (Colin, 1992; Colin[21]).

Epinephelus itajara No information.

3.34 Predators

Epinephelus striatus Information on predation upon groupers is largely lacking, although sharks attacked Nassaus at spawning aggregations in the Virgin Islands (Olsen and LaPlace, 1979) and there is one report of cannibalism in this species (Silva Lee, 1974). No predation was observed on spawning fish in the Bahamas, despite the presence of sharks in the area (Colin, 1992). One mutilated fish was recovered, possibly attacked by a barracuda or shark following release of tagged, laboratory-reared, naive individuals onto a reef in the Virgin Islands (Roberts et al., 1995). Early post-settlement juvenile preferences for macroalgae over seagrass beds is probably related, in part, to higher levels of predation in seagrass beds (Nadeau and Eggleston, 1996).

Epinephelus itajara Sharks have attacked juvenile jewfish that were caught on set lines in the mangrove shorelines of southwest Florida, in the Gulf of Mexico (Eklund, personal observ.). No other information on predators of jewfish has been documented.

3.35 Parasites, diseases, and abnormalities

Epinephelus striatus Parasites occur in both wild-caught and cultivated Nassau grouper, predominantly in the viscera and gonads. Encysted larval tapeworms are common in the viscera and a reddish-brown nematode occurs in the gonads (Thompson and Munro, 1978). Parasitic isopods are found in nostrils (Thompson and Munro, 1978). The digenetic trematodes *Helicometra torta* (pyloric caeca), *Lecithochirium parvum* and *L. microstomum* (stomach), and *Sterrhurus musculus* (stomach) were identified in Florida-caught fish (Manter, 1947; Overstreet, 1969).

Diseases and abnormalities are not described. Although several species of western Atlantic groupers are known to be ciguatoxic (especially when large), Nassau groupers seem to be uniformly non-toxic throughout their range (Halstead, 1967; Jory and Iverson, 1989) with the interesting exception of one small toxic Nassau grouper in the Virgin Islands (Brownell and Rainey, 1971). Excrescences were noted on otoliths and one fish had a completely malformed sagittal pair with the whole of the concave surface overgrown with a large excrescence (Thompson and Munro, 1978).

Epinephelus itajara Parasites associated with the jewfish include: trematoda—*Lecithochirium microstomum, Prosorhynchus promicropsi, Stephanostomum promicropsi*; nematoda—*Heterotyphlum eurycheilum, Hysterothylacium* sp.; hirudinea—*Trachelobdella* sp.; isopoda—*Excorallana tricornis, Nerocila acuminata, Rocinela signata*; copepoda—*Grandiungus promicrops, Tuxophorus caligodes* (Bullock et al., 1992). Breder and Nigrelli (1934) reported *Myrichthys acuminatus* from the coelom of a jewfish. *Vibrio parahaemolyticus* was isolated from a single jewfish (Monsreal and Flores-Abuxapqui, 1988).

From 1989 to 1991, 8 large jewfish (1,702–2,056 mm TL) from southwest Florida and the Florida Keys were found with average mercury concentrations exceeding the U.S. Food and Drug Administration's action level of 1 ppm methyl mercury. The range was between 0.42–3.3 total mercury concentration, with a tendency for larger individuals to have higher concentrations (Henderson[22]).

3.4 Nutrition and growth

3.41/3.42 Feeding and food

Epinephelus striatus Groupers are unspecialized, bottom-dwelling, solitary predators (Randall and Brock, 1960; Randall, 1965). Feeding takes place throughout the diel cycle although most fresh food is found in stomachs collected in the early morning and at dusk (Randall, 1967). Empty stomachs were also noted throughout daylight hours (Silva Lee, 1974). Individuals feed by rapidly dilating the gill covers to engulf prey by suction (Thompson and Munro, 1978; Carter, 1986) and take a wide variety and size range of fishes and invertebrates, both benthic and pelagic (Tables 4 and 5). With increasing age, there is a shift from consuming crustaceans to taking fishes, larger bivalves, lobster, and gastropods (e.g. Eggleston et al., 1998). However, the relationship between fish size and prey size shows much variation, with large fish eating small prey and vice versa. For instance a 580 mm FL Nassau grouper swallowed a 620 mm

[20] Dunham, Jason. Caribbean Marine Research Center, c/o Florida State Marine Laboratory, Rte. 1, Box 456, Sopchoppy, FL 32358. Unpubl. report to the Caribbean Marine Research Center, 29 March, 1989.

[21] Colin, Pat. 1990. Coral Reef Research Foundation, P.O. Box 1765, Koror, Palau 96940. Personal commun.

[22] Henderson, George. 1992. Florida Marine Research Institute, 100 8th Avenue, SE, St. Petersburg, FL 33701. Personal commun.

Table 4

Food items recorded in the stomachs of the Nassau grouper, *Epinephelus striatus* (from Randall, 1965, 1967; Silva Lee,1974; Claro et al., 1990; Carter et al., 1994).

Nekton
- Fishes
  - Acanthuridae
    - *Acanthurus* sp.
    - *Acanthurus coeruleus*
  - Apogonidae
  - Atherinidae
  - Balistidae
    - *Balistes vetula*
  - Bothidae
  - Carangidae
    - *Caranx ruber*
  - Clupeidae
    - *Harengula humeralis*
    - *Harengula clupeola*
    - *Jenkinsia lamprotaenia*
  - Gerreidae
    - *Gerres cinereus*
  - Haemulidae
    - *Haemulon aurolineatum*
    - *Haemulon flavolineatum*
    - *Haemulon album*
    - *Haemulon sciurus*
    - *Haemulon plumieri*
    - *Haemulon* sp.
  - Holocentridae
    - *Sargocentron vexillarium*
    - *Myripristis jacobus*
    - *Holocentrus rufus*
    - *Holocentrus* sp.
  - Labridae
    - *Halichoeres garnoti*
    - *Halichoeres bivittatus*
    - *Halichoeres* sp.
    - *Hemipteronotus* sp.
    - *Clepticus parrae*
  - Lutjanidae
    - *Lutjanus synagris*
    - *Lutjanus* sp.
    - *Ocyurus chrysurus*
  - Monacanthidae
    - *Monacanthus ciliatus*
    - *Monacanthus* sp.
    - *Cantherines pullus*
  - Mullidae
    - *Pseudupeneus maculatus*
  - Muraenidae
    - *Gymnothorax moringa*
    - *Gymnothorax* sp.
    - *Enchelycore nigricans*
    - *Lycodontis moringa*
    - *Muraena miliaris*
    - *Muraena* sp.
  - Ostraciidae
    - *Lactophrys* sp.
  - Pomacentridae
    - *Chromis cyanea*
    - *Chromis multilineata*
    - *Pomacentrus fuscus*
    - *Pomacentrus* sp.
    - *Abudefduf saxatilis*
    - *Microspathodon chrysurus*
  - Priacanthidae
    - *Priacanthus cruentatus*
  - Scaridae
    - *Sparisoma aurofrenatum*
    - *Sparisoma rubripinne*
    - *Sparisoma chrysopterum*
    - *Sparisoma* sp.
    - *Scarus vetula*
    - *Scarus croicensis*
    - *Scarus* sp.
  - Serranidae
    - *Hypoplectrus puella*
    - *Cephalopholis fulva*
    - *Epinephelus striatus*
  - Synodontidae
    - *Synodus intermedius*
    - *Synodus* sp.
  - Urolophidae
    - *Urolophus jamaicensis*
- Molluscs
  - Squids
    - *Loligo* sp.
  - Cuttlefish, octopi

Benthic animals
- Molluscs
  - Gastropods
    - *Strombus gigas*
    - *Strombus* sp.
    - *Fasciolaria tulipa*
  - Bivalves
    - *Barbatia cancellaria*
  - Pelecypods
- Crustaceans
  - Isopods
  - Stomatopods
    - *Gonodactylus perstedi*
    - *Pseudosquilla ciliata*
    - *Squilla* sp.
  - Shrimps/prawns
    - Alpheids
    - Carideans
    - Penaeids
  - Lobsters
    - *Panulirus argus*
    - *Panulirus guttatus*
    - *Justitia longimana*
    - *Palinurellus gundlachi*
  - Hermit crabs
    - *Paguristes depressus*
    - *Petrochirus diogenes*
  - Crabs
    - *Calappa flammea*
    - *Calappa* sp.
    - *Stenorhynchus seticornis*
    - *Mithrax verrucosus*
    - *Mithrax cinctimanus*
    - *Mithrax* sp.
    - *Macrocoelema* sp.
    - *Petrolisthes galathinus*
    - *Chronus ruber*
    - *Portunus sebae*
    - *Portunus* sp.
    - Xanthids
    - Grapsids

Gymnothorax; overall, mean prey size was 15% of the Nassau grouper FL (Silva Lee, 1974).

Four studies provide a feeding profile of the Nassau grouper (Table 5). Fish predominated, with scarids and labrids most commonly identified, possibly because the former can be readily recognized from stomach contents by their unique dentition (Randall, 1965). Crabs were the most common invertebrates. Although hermit crabs and the operculae of *Strombus* and *Fasciolaria* were found, stomachs did not contain shells. In one Cuban study, the most abundant items (by weight) were grunts, parrotfishes, and octopus with a suggestion that more grunts were taken in winter months (Claro et al., 1990). In Belize, the predominant food, by percentage frequency of occurrence, was fish, with a high percentage of crustaceans, especially crabs, and a small number of gastropods, cephalopods, and pelecypods. The principal prey fish families were grunts and snappers (Carter et al., 1994).

Like other groupers, Nassaus follow and feed with predators, such as triggerfish, octopus, or eel (Carter et al., 1994; Sullivan and de Garine-Wichatitsky, 1994; Rob-

Table 5

Principal categories of food items encountered in the stomachs of Nassau grouper, *Epinephelus striatus*, in four studies: (A) Virgin Islands (Randall, 1965, percent by volume); (B) Cuba (Silva Lee, 1974, percent frequency occurrence); (C) Cuba (Claro et al., 1990, percent by weight); (D) Belize (Carter et al., 1994, percent frequency occurrence).

Food category	A	B	C	D
Nekton, fish	53	39	71	58
Benthic, crustaceans				
crabs	23	29	8	16
stomatopods	6	3	<1	1
shrimp/prawn	5	8	<1	3
spiny lobster	4	6	4	6
hermit crab	1	<1	—	1
isopod	<1	<1	—	—
unidentified	1	4	—	3
Nekton, molluscs				
cephalopods	5	9	15	6
Benthic, molluscs				
gastropods	2	2	2	1
Unidentified	—	—	—	5

erts et al., 1995; Sadovy, personal observ.) presumably benefiting from spoils made available directly, or from disturbance of prey species.

Although adult Nassaus are unspecialized predators, early life-history phases exhibit a high degree of trophic plasticity with evidence of filter feeding, particulate feeding, and piscivory (Grover, 1993, 1994). Pelagic-phase Nassau grouper feed on pteropods, amphipods, and copepods, especially *Corycaeus* spp., which comprised approximately 40% of identifiable items found in one study (Greenwood, 1991; Grover et al., 1998). Pelagic early-juvenile Nassau grouper (20.2–27.2 mm SL) take food items ranging from dinoflagellates (±99% by number) to fish larvae and mysids (28–79% by volume).

Epinephelus itajara Although predation on relatively slow-moving fishes and invertebrates indicates that the jewfish's large size and sluggish nature typically define its prey selection, it is able to accelerate from a resting position with explosive speed (Bullock and Smith, 1991). Poor development of canine teeth in this species is a reflection of its crustacean diet, although the jewfish does take fish bait (Smith, 1971).

Crustaceans, particularly spiny and slipper lobster and crab, form an important part of the diet of jewfish (Longley and Hildebrand, 1941; Randall, 1983) although fishes and hawksbill turtles have also been found in stomachs (Randall, 1983). Juveniles consume shrimp (including pink shrimp, *Penaeus duorarum*), xanthid crab, *Rhithropanopeus harrisii*, and sea catfish, *Arius felis* (Odum, 1971; Bullock and Smith, 1991). Randall (1967) analyzed the stomach contents of nine fish (1,250–1,650 mm SL) and found 69% (by volume) of the diet consisted of lobsters (*Panulirus argus* and *Scyllarides aequinoctialis*), while fish (*Dasyatis americana* and *Diodon* sp.), crabs, and sea turtles made up 13%, 12%, and 6% of the diet, respectively. Fish taken in Puerto Rico contained the crab, *Carpilius carallinus*, Spanish and spiny lobsters, *Diodon* spp., and stingrays (Erdman[23]).

Jewfish stomach contents from the eastern Gulf of Mexico included the following: octopus mouthparts; gastropod, *Fasciolaria tulipa*; lobsters, *Panulirus argus*, *Scyllarides* sp.; crabs, *Calappa flammea*, *Menippe mercenaria*, *Ovalipes floridanus*, *Callinectes* sp., *Hepatus* sp.; and fishes, *Chaetodipterus faber*, *Lactophrys quadricornis*, *Etrumeus teres*, and *Chilomycterus schoepfi* (Bullock and Smith, 1991).

3.43 Growth rate

Epinephelus striatus Growth in Nassau grouper has been examined by size-frequency analyses, tagging studies, field observations, and by sagittal otoliths. Most studies indicate rapid growth, about 10 mm/month for small juveniles, until sexual maturity at about 4–6 years, slowing to about 2mm/month, or less, in larger or sexually mature fish (Fig. 16).

Mean monthly growth of Nassau juveniles on artificial and natural reefs in the Virgin Islands was 8.4 to 11.7 mm/month (determined during six visual censuses over 11 months) for juveniles 30–270 mm TL (Beets and Hixon, 1994). Similarly, juveniles sampled at Lee Stocking Island in the Bahamas grew at about 10 mm/month between 32 and 85 mm TL (Eggleston, 1995).

The growth zones deposited in otoliths were validated as annual using oxytetracycline (OTC) marking techniques; otolith legibility was approximately 80–95% (Bush et al., 1996). Marginal increment analysis of the sagittal otoliths also suggested that growth zones were formed annually and that annual increment deposition occurred from April to May (Claro et al., 1990).

Data from scales and otoliths indicate that fish reach 400–450 mm SL (i.e. sexual maturity) in approximately 4–7 years. However, estimates of size-at-age derived from length-frequency data suggest more rapid growth (Olsen and LaPlace, 1979) (Table 6). This apparent discrepancy between otolith- and length-based methods of age determination could result from the unavailability of age class 1 individuals in the fishery, resulting in older (i.e. age 2+ years) individuals designated as age 1 year. Von Bertalanffy growth parameters derived for the Nassau grouper with the Brody growth coefficient (K) range from 0.063–0.185 (Table 7).

[23] Erdman, Don. 1989. 890 NE 90th Avenue, Portland, OR 97220. Personal commun.

Table 6

Epinephelus striatus size-at-age data for ages 1-13 years. All lengths are in mm (standard/SL or total/TL lengths as indicated). Ageing method is given.

	Age (years)												
Source	1	2	3	4	5	6	7	8	9	10	11	12	13
a	293	354	390	464	537	561	634	659	—	—	—	—	—
b	160	270	—	410	480	540	570	600	640	650	660	700	710
c	175	253	309	358	401	436	468	497	519	542	563	580	591
d	174	254	315	366	414	451	483	518	559	583	594	617	—
e	235	370	435	500	543	605	660	720	760	800	—	—	—

a: Buesa, 1987; Cuba, aged by scales/TL.
b: Bush et al., in press; Cayman Islands, aged by otoliths/TL lengths estimated from observed growth curve.
c & d: Claro et al., 1990; SW and NE Cuba, respectively, fish from both areas were aged by otoliths and backcalculation/TL.
e: Olsen and LaPlace, 1979; Jamaica, aged by length-frequency data/SL.

Table 7

Von Bertalanffy growth equation parameters for Nassau grouper, *Epinephelus striatus*. Standard equation for length-at-age is: $L_t=L\infty(1-e^{-k(t-t_0)})$. Lengths are in cm (length type indicated).

		Parameter			
Source & method	Locality	Length type	L∞	t_0	K
Olsen & LaPlace, 1979	Virgin Islands	SL	97.4	0.488[1]	0.185
Claro et al., 1990	Cuba (SW)	TL	94.0	–3.27	0.063
	Cuba (NE)		76.0	–1.12[2]	0.127
Thompson & Munro, 1978	Jamaica	TL	90.0[3]	—	0.090
Baisre & Páez, 1981	Cuba	—	92.8	—	0.100

[1] Appears also as $t_0 = -0.488$ in some places.
[2] Appears also as –4.13 in Abstract.
[3] L∞ assumed, based on tagging data from Randall, 1962, 1963.

Growth rates were also determined by field observations and tagging studies. In the Virgin Islands, animals tagged for less than 300 days yielded the following growth rates: 175–250 mm TL grew about 4.55 mm/month; 251–325 mm TL about 3.5 mm/month; 326–451 mm TL about 1.92 mm/month (Table 8) (Randall, 1962). However, growth rates were evidently underestimated because of growth suppression due to tagging (Thompson and Munro, 1978). Fish that remained in the field for 313 to 737 days had higher growth rates, varying from 4 to 6.6 mm/month for fish in the 256–380 mm TL size. Growth in Nassau grouper was also measured by calculating weight increments of marked fish in the field: weight increase for 7 individuals in the 700 g size class was 20–50% per year with an average of 38% (Bardach and Menzel, 1957). Data suggested a decline in growth rate after jaw tags were applied.

Length-weight relationships for standard (Fig. 17), total, and fork lengths, and TL-SL relationships are shown in Table 9.

Epinephelus itajara Age in jewfish ranging in size from 100 to 2,200 mm TL was determined from sectioned otoliths (sagittae); fish attained a maximum of 37 years, assuming that temporal validation of growth zones applies equally to all age classes. For ages 1–10 years, opaque zones in sectioned sagittae form annually between April and August, as determined by both marginal increment analyses and OTC marking of two individuals, ages 3 and 4 years, maintained in captivity for 11 and 22 months, respectively (Bullock et al., 1992). Otolith legibility was almost 100%.

Fish grew slowly after age 7 years (Bullock et al., 1992). Average annual growth through age 6 was greater than

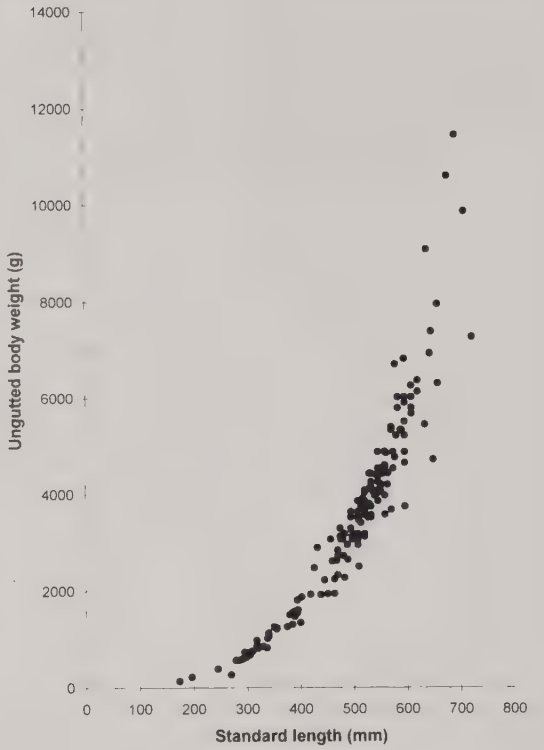

Figure 17
Length-weight relationship of the Nassau grouper, *Epinephelus striatus*, captured in the Bahamas between 1988 and 1990; Log Ungutted Weight (g) = –4.67 + 3.03 Log Standard Length (mm); n=186; r^2=0.97; p<0.001 (Sadovy and Colin, 1995, and unpublished data).

100 mm/year, declining to about 30 mm/year by age 15, and to less than 10 mm/year after age 25 (Fig. 18). Von Bertalanffy growth parameters calculated for the jewfish, both males and females combined, yielded K = 0.13/year, $L\infty$ = 2,006 mm TL and t_o = -0.49 years. There was no significant difference between the sexes in growth parameters (Bullock et al., 1992).

Length-weight relationships for standard (Fig. 19), total, and fork lengths, and TL-SL relationships are shown in Table 9.

3.5 Behavior

3.51 Migrations and local movements

Epinephelus striatus Nassau grouper are solitary and, while they remain in specific areas for extended periods (Bardach, 1958), they may exhibit distinct ontogenetic movements, especially as juveniles (Section 2.1).

Table 8
Growth of tagged-recaptured *Epinephelus striatus* in the Virgin Islands (from Randall 1962, 1963). Lengths are total lengths in mm.

Length at tagging	Length at recovery	Tagging period	Growth per month/mm
175	180	78	1.95
195	264	513	4.08
196	200	70	1.74
198	207	47	5.82
204	252	273	5.33
204	220	55	8.96
213	230	134	3.87
230	241	38	8.80
232	256	168	4.35
237	238	44	0.67
246	255	78	3.51
250	297	257	5.56
252	252	33	0.00
254	317	288	6.64
255	295	509	2.39
276	280	104	1.17
280	286	49	3.72
292	301	108	2.54
295	330	136	7.84
298	304	92	1.98
299	304	39	3.91
302	322	103	5.90
302	332	161	5.67
307	314	80	2.56
309	366	52	3.33
314	311	39	0.00
314	321	106	2.01
314	355	215	5.78
316	322	102	1.78
320	324	80	1.52
325	327	78	0.75
330	333	42	2.17
340	341	42	0.72
343	348	177	0.86
357	365	127	1.91
358	365	49	4.34
364	372	105	2.32
378	382	62	1.96
410	413	55	1.66
451	455	70	1.74
225	266	313	4.00
229	334	737	4.40
240	338	661	4.40
245	333	674	4.40
250	380	667	5.80

Over 12 months, in one area, there was a gradual turnover of individuals until the original population had been replaced (Bardach, 1958). They are able to home to residential reefs over short distances based on visual

Table 9

Length-weight and length-length parameters for *Epinephelus striatus* and *E. itajara*. The length-weight relationship is defined as: $W=aL^b$, where L is length (standard/SL, fork/FL or total/TL, as indicated) in mm and W is body weight in grams (gutted, G, or ungutted, UG, as indicated—where known). The standard length-total length relationship is defined as: TL=a+bSL.

Locality	Restrictions[1]	Parameter a	Parameter b	Source
Length-weight				
Epinephelus striatus				
Virgin Islands	180-760 (SL) n=241	0.0097	3.23	Olsen and LaPlace, 1979
(St. Thomas/St. John)	330-770 (SL) n=73	1.43×10^{-6}	3.38	Bohnsack and Harper, 1988 (UG)
Puerto Rico	210-645 (FL) n=60	1.26×10^{-5}	3.04	Bohnsack and Harper, 1988 (UG)
Cuba (NE)	n=75 (TL)	0.1980	2.98	Claro et al., 1990
Cuba (SW)	n=270 (TL)	0.0052	3.30	Claro et al., 1990
Jamaica	325-825 (TL) n=112	0.0107	3.11	Thompson and Munro, 1978 (UG)
Belize	180-802 (SL) n=930	0.0107	3.08	Carter et al., 1994 (UG implied)
Florida	203-516 (TL) n=9	3.8×10^{-6}	3.23	Bohnsack and Harper, 1988 (UG)
Bahamas	174-724 (SL)	2.14×10^{-5}	3.03	Sadovy and Colin, 1995 (UG)
Epinephelus itajara				
Gulf of Mexico	75-2160 (TL) n=402 (TL)	2.94×10^{-5}	2.94	Bullock et al., 1992 (G)
Gulf of Mexico	n=66 (TL)	3.056×10^{-8}	1.31	Bullock et al., 1992 (UG)
Total length-standard length				
Epinephelus striatus				
Cuba	n=330	2.24	1.11	Claro et al., 1990
Jamaica	430-750 n=26	3.00	1.09	Thompson and Munro, 1978
Bahamas	174-695 n=33	2.81	1.13	Sadovy and Colin, 1995
Epinephelus itajara				
Gulf of Mexico	—	32.45	1.18	Lew Bullock, text footnote 9

[1] Restrictions are upper and lower sizes in samples analyzed.

cues; blinded fish do not home (Bardach, 1958). Ten recaptures, out of 11 fish originally tagged in Bermuda, demonstrated homing between isolated patch reefs separated by 100 m of sandy substrate. The greatest distance traveled was 16 km in 12 days (Randall, 1962, 1963). In the Florida Keys and the Virgin Islands, tagged, translocated fish exhibited strong home-reef specificity (Beaumariage and Bullock, 1976; Beets and Hixon, 1994). Twenty-seven tagged, 31-month old fish (310–380 mm TL), which had been raised from eggs in captivity, survived at least 200 days in the field with one fish moving 12 km in eight days (Roberts et al., 1995). In the Bahamas, juveniles moved from inshore areas offshore to natural and artificial reefs within a year of settlement out of the plankton (Eggleston, 1995).

Nassau groupers are diurnal or crepuscular in their movements (Collette and Talbot, 1972) and do not usually move far from cover (Starck and Davis, 1966). Three sonically tagged fish were most active in the hours prior to and following sunrise and sunset; two of the fish moved randomly within a 160 m × 80 m rectangle during the day, returning in the evening to where they had initiated daily activities (Carter et al., 1994). Sullivan and de Garine-Wichatitsky (1994) estimated that individu-

als moved at least 400 m/day and 20 m or more from their home reefs.

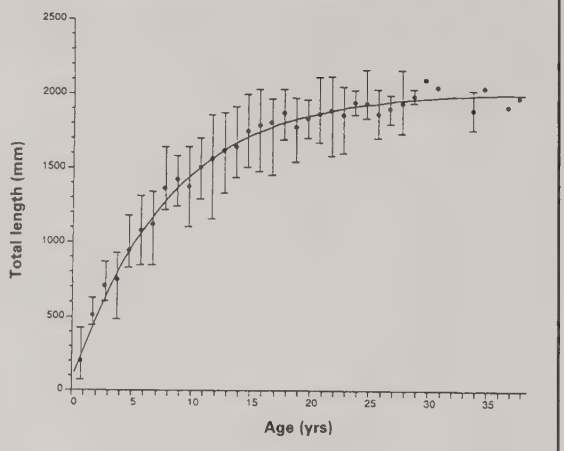

Figure 18
Observed ages (years), total lengths (mm), and predicted growth model for jewfish, *Epinephelus itajara*, collected from the eastern Gulf of Mexico (n=382) (from Bullock et al., 1992).

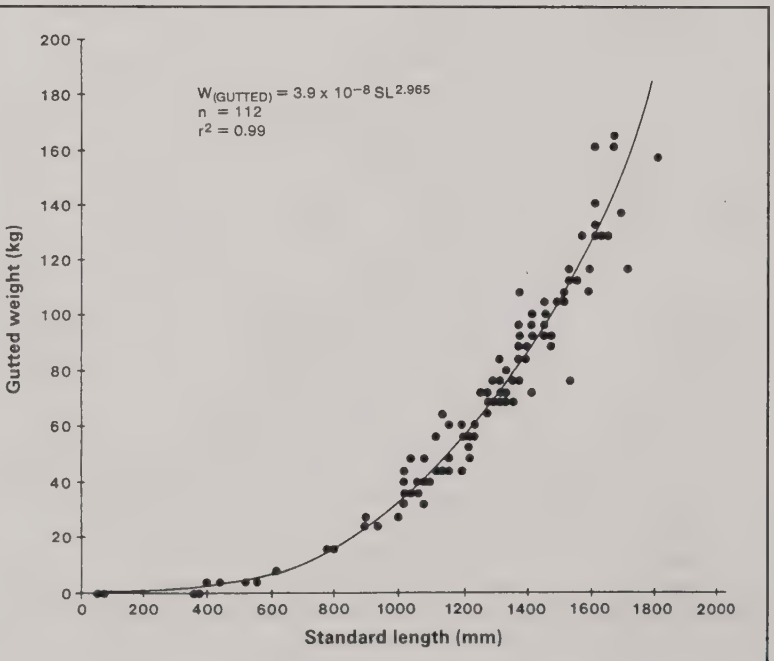

Figure 19
Length-weight (gutted) relationship of the jewfish, *Epinephelus itajara*, captured in the eastern Gulf of Mexico (from Bullock and Smith, 1991).

Movement away from resident reefs occurs as spawning time approaches and distances traveled to an aggregation site can be substantial. Observations of migrating groups of fish ("corridas"), on or before the full moon of spawning, indicate that at least some fish travel to aggregation sites in groups ranging from a few fish up to about 500 individuals (Colin, 1992) (see also Section 3.16). Several dozen fish were observed passing slowly along the 30–40 m shelf break contour at several localities along a reef in Belize in late October and early November (Carter et al., 1994), i.e. a month or two before spawning was likely. One tagged fish moved at least 110 km in two months to an aggregation site in the Bahamas (Colin, 1992). Another fish, tagged on an aggregation site in Belize, was recaptured 2 years later 240 km north of the tagging site (Carter et al., 1994).

Observations suggest that individuals can return to their original home reef following spawning; several large adult Nassaus in the Bahamas, clearly swollen with gametes, disappeared from residential areas for periods ranging from 10 days before, to a few days after, the full moon of December 1989. The same fish returned visibly slimmer. They remained in home areas for the January 1990 full moon and were seen neither to swell with gametes nor to exhibit courtship behavior, suggesting that not all mature fish aggregate in every aggregation month in each reproductive season (Colin[21]). In Honduras, groupers normally located 48 km from an aggregation site disappeared from resident reefs at spawning time (Fine, 1992).

Epinephelus itajara Jewfish apparently stay within circumscribed areas for up to one year (Smith, 1976) with large individuals found both inshore and offshore. During the spawning season, jewfish aggregate at specific locations, although it is not known what distance is traveled to reach aggregation sites. Of 217 adult jewfish tagged at spawning sites in southwest Florida in 1996–97, 5 were re-sighted although fish tagged on one trip were not observed at the same site on the next trip. One fish tagged at one aggregation site was sighted at another, 6 km away, on the next day. Outside of aggregations, jewfish showed strong site fidelity (Koenig et al.[18]).

3.53 Responses to stimuli

Epinephelus striatus Little is known of responses to stimuli in the Nassau

grouper, with the exceptions of responses related to crowding, sound generation, reproduction, and cleaning behavior. This species is noted for a negative rheotropic response when confined and crowded; heads are oriented away from flowing water, possibly to protect the lips which are the most sensitive integumentary region (Jordan, 1917). Although this species tends to be solitary, individuals will crowd peaceably in caves (Silva Lee, 1974) or in fish traps (Sadovy, personal observ.), with some proclivity to re-enter fish traps resulting in multiple recaptures (Randall, 1962).

The Nassau grouper produces a loud grunting sound which can be heard with the unaided ear. The sound is produced by contraction of bilateral muscles in the region directly behind the opercles and around the air bladder (Moulton, 1958). In aquaria, they emit deep booms and sustained rumbles as single grunts or in rapid series (Fish and Mowbray, 1970). In the field, occasional grunts or "plop" sounds are produced in response to specific stimuli, such as being disturbed by divers (Hazlett and Winn, 1962; Fish and Mowbray, 1970; Bright, 1972; Nagelkerken, 1981). Acoustical characteristics of the sounds range from <85 cps to about 2,000 cps, with sound duration varying from 51.0 to 124.0 ms (Hazlett and Winn, 1962). Nassaus responded to irregularly pulsed signals designed to attract sharks, off the Bahamas, approaching the sound source slowly and moving away 10–30 seconds later (Myrberg et al., 1969).

Nassau grouper are frequently involved in symbiotic cleaning behavior at cleaning stations on coral reefs; species that clean them include several gobies, *Gobiosoma* spp., and shrimp that remove gnathiid isopods from the body, fins, gill chambers, and mouth (Collette and Talbot, 1972; Böhlke and McCosker, 1973; Darcy et al., 1974; Sargent and Wagenbach, 1975; Sullivan and de Garine-Wichatitsky, 1994). Interestingly, naive Nassau grouper raised in captivity in the absence of cleaners, allowed cleaning by *Gobiosoma evelynae* and by *Stenopus hispidus* and *Periclimenes* spp. within one hour of release onto a coral reef (Roberts et al., 1995). Movements and activity patterns of Nassaus were significantly influenced by the position of cleaning stations in the Bahamas (Sluka and Sullivan, 1996; Sluka et al., 1997a).

Epinephelus itajara Little is known of jewfish responses to stimuli although they often produce sounds, submit to cleaning behavior, and may approach divers. One large individual made a tremendous boom, sometimes followed by two smaller grunts, whenever prodded; two large fish made no spontaneous grunts but emitted several loud bursts when pursued by a diver (Fish and Mowbray, 1970). The swimbladder and associated muscles are believed to provide the sound-producing mechanism (Fish and Mowbray, 1970). Sonic activity is associated with courtship behavior; during an August full moon period at a wreck off the Florida coast, a presumed male approached presumed females and boomed several times (Colin, 1994). Cleaning gobies were observed removing parasites from the mouth of a jewfish in Puerto Rico (Mandojana, 1983). Large jewfish have been reported to approach divers closely (Zinkowski, 1971) and are not wary, making them highly susceptible to spearfishing.

4 POPULATION

4.1 Structure

4.11 Sex ratio

Epinephelus striatus The sex ratios of adult Nassau grouper in relatively undisturbed populations seldom differ markedly from unity. However, there are generally more females than males at exploited spawning sites compared to unexploited sites, suggesting that sex-selective fishing may occur during either aggregation or non-aggregation periods (Table 10) (Carter et al., 1994; Sadovy and Colin, 1995). The most biased adult sex ratio reported is 4:1 (F:M) in heavily exploited areas in Cuba, although the authors stated that if all "intersexes" (term not defined) had been counted as males, the sex ratio would be 1:1 (Claro et al., 1990). Given the bisexual juveniles found in this species, sex assignment of young fish could well have been in error, greatly overestimating female numbers (Section 3.11).

Care is needed in assessing sex ratios at aggregations, however, because of possible gear selectivity, differences between the sexes in time spent at aggregation sites, or migration patterns. For example, in Bermuda in early July, only 20% of individuals moving towards the aggregation site were females, but by late July the proportion of females had risen to 36%; either males precede the females to spawning sites, or females do not enter fish traps until the onset of spawning, as some fishers believe (Bardach et al., 1958).

Epinephelus itajara The only information on sex ratios is a finding of 1.75:1 (F:M) in the eastern Gulf of Mexico, from samples taken periodically from commercial and recreational catches between 1977 and 1990 (Bullock et al., 1992).

4.12 Age composition

Epinephelus striatus Nassau grouper attain 29 years with sexual maturation occurring at 4 years or above; fish taken commercially generally fall within age classes 2–9 years and include many immature individuals; no age differences at size between males and females were noted (Bush et al., 1996) (Section 5.42) (Table 3). Over 80%

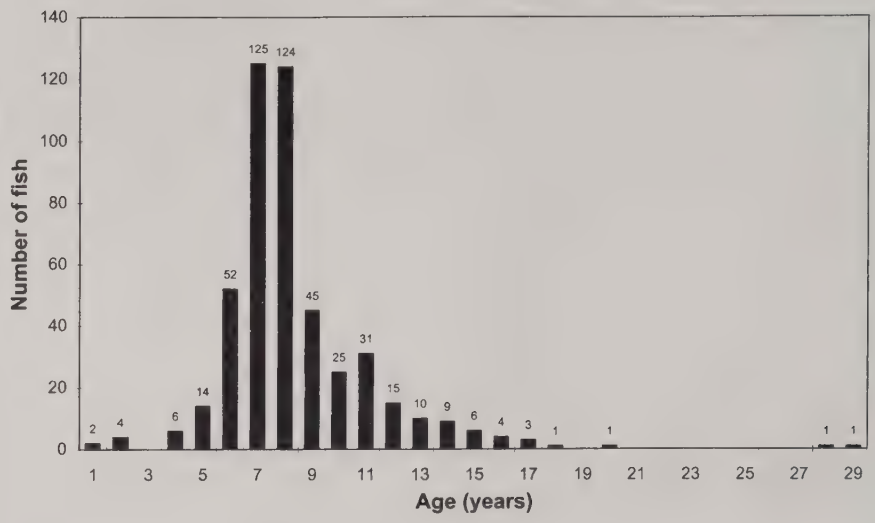

Figure 20

Age frequency distribution of Nassau grouper, *Epinephelus striatus*, caught at 5 aggregations off the Cayman Islands from 1987 to 1992 (Bush et al., in press; with permission).

Table 10

Mean sizes and sex ratios of aggregating and non-aggregating Nassau grouper, *Epinephelus striatus*, in the western Atlantic, from lightly (top of table) to heavily (bottom of table) exploited areas. Fishing intensity implied by descriptions of current and historic fishing activity (from Sadovy and Colin, 1995). Number in parentheses refers to references.

Sex ratio F:M	Mean SL in mm F	Mean SL in mm M	Max SL in mm	Gear used[1]	Location and source[2]
0.57:1 (n=750)	526	529	750	T,H	Bermuda, offshore banks > 60 m deep (1)
0.72:1 (n=163)	554[3]		718	H,T	Jamaica, offshore (3)
1.5:1 (n=694)	517	521	802	H,S	Belize, aggregation (4)
2.0:1 (n=42)	502	487	568	G	Mexico, aggregation (2)
0.67:1 (n=70)	514	503[4]	657	G	Mexico, aggregation (2)
1.0:1 (n=940)	589	585	940	T,H	U.S.V.I., aggregation (5)
1.9:1 (n=95)	516	512	640	H	Caymans, aggregation (6)
2.0:1 (n=140)	506	538	772	H	Caymans, aggregation (7)
2.2:1 (n=717)	418	420	760	H,S	Belize, nonaggregated(4)
2.4:1 (n=485)	418	420	690	H,S	Belize, aggregation (4)
2.5:1 (n=216)	549	517[4]	700	T	Bahamas, aggregation (8)
4.0:1 (n=319)	>500[3]		710	S,T	Cuba, (9) (only adults assessed)

[1] Gear used: T=trap; H=handline; S=spear; G=gillnet.

[2] Sources: (1) Bardach et al., 1958; (2) Sosa-Cordero & Cárdenas-Vidal ,1997; Aguilar-Perera, 1994; (3) Thompson & Munro, 1978; (4) Carter et al., 1994; (5) Olsen and LaPlace, 1979; (6) Colin et al., 1987; (7) Bush (text footnote 42); (8) Colin, 1992; (9) Claro et al., 1990.

[3] Males and females combined.

[4] Females significantly larger than males at $p<0.05$, otherwise no sex difference in size.

of the samples from an aggregation in the Virgin Islands were aged 4–6 years (as estimated by probit analysis) (Olsen and LaPlace, 1979), while most fish taken at the aggregations in the Cayman Islands were aged 7–8 years (Fig. 20). Age classes 6–9 dominated in southwestern Cuba and 3–8 years in northeastern Cuba (Claro et al., 1990).

Epinephelus itajara In samples taken from the eastern Gulf of Mexico, male and female age at size overlapped

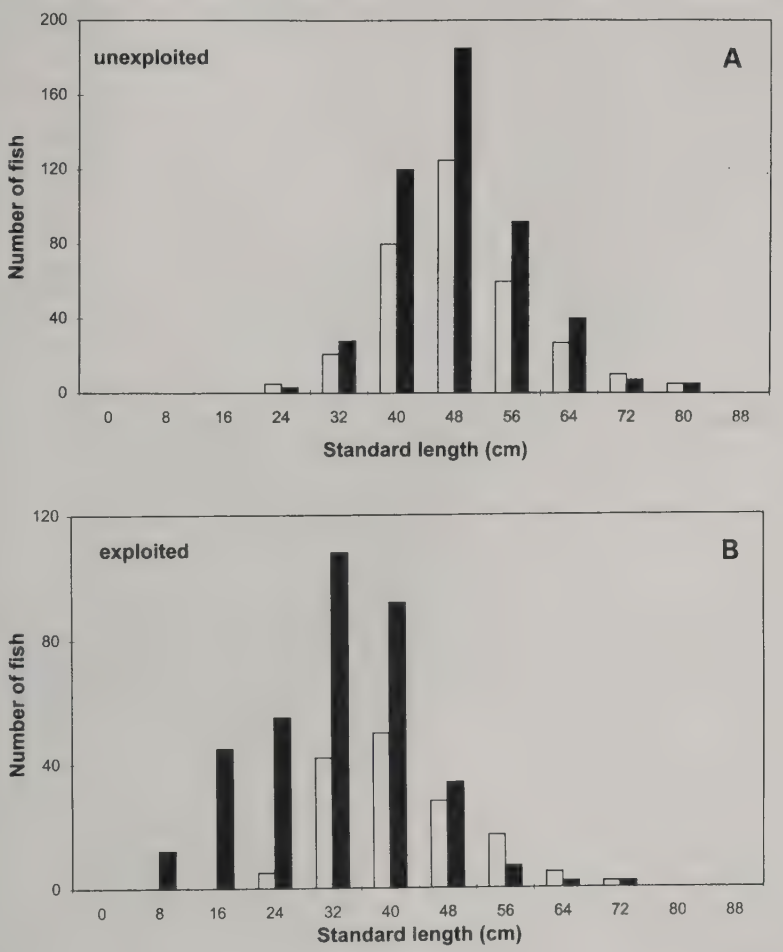

Figure 21
Length-frequency distributions of male and female Nassau grouper, *Epinephelus striatus*, taken from aggregations [males = white bars, females = black bars] in Belize: (A) unexploited site (n=694); (B) exploited site (n=485) (Carter et al., 1994).

and the majority of individuals were between 9 and 15 years. Few fish exceeded 30 years (Bullock et al., 1992).

4.13 Size composition

Epinephelus striatus A maximum length of 1,220 mm TL and weight of 23–27 kg are recorded for the Nassau grouper (Evermann, 1900; Randall, 1963; Smith, 1971; Buesa, 1987). Most fish at markets, however, are considerably smaller (i.e. 2–11 kg). Weights of aggregating fish ranged from 5–12 kg, with a maximum of 14 kg (Böhlke and Chaplin, 1968; Smith, 1971, 1978; Aguilar-Perera, 1994). Grouper up to 960 mm SL were taken in the Virgin Islands although fish larger than about 700 mm were uncommon (Olsen and LaPlace, 1979). Maximum theoretical mean length ($L\infty$ from the von Bertalanffy growth function–von Bertalanffy, 1957) has been estimated at between 760–1,129 mm TL (Thompson and Munro, 1978; Olsen and LaPlace, 1979; Claro et al., 1990).

Mean male and female sizes are similar within a given area, or at a specific aggregation site, with some indication that sizes of both sexes decline in areas of higher exploitation within a specific region (Table 10). When exploitation is high, catches are largely comprised of juveniles. For example, in Belize, the average length of both sexes was 100 mm smaller in catches from exploited compared to unexploited aggregations (Fig. 21). In only two cases were females significantly longer than males,

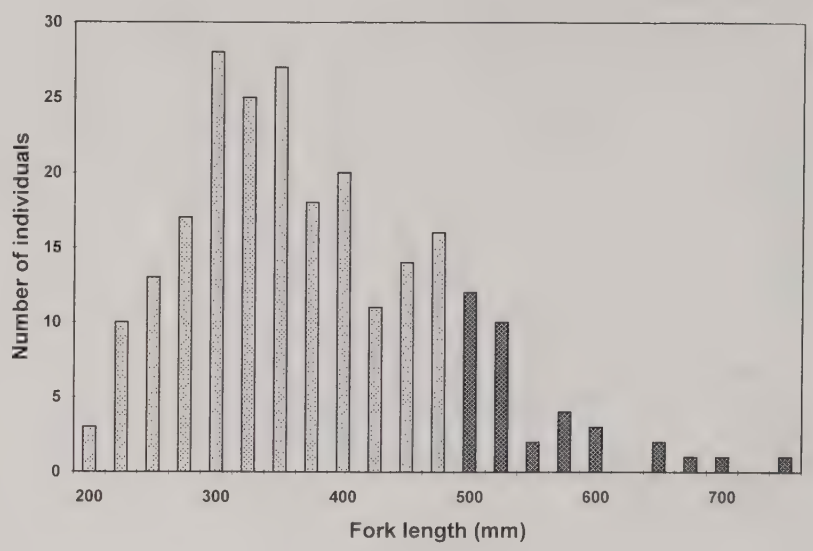

Figure 22
Length-frequency distribution of Nassau grouper, *Epinephelus striatus*, from commercial fishery landings in Puerto Rico between 1986 and 1990. Light stipple=immature; dark stipple=mature. Source: Puerto Rico Fisheries Research Laboratory, Department of Natural Resources, State/Federal Fishery Program.

while males were never larger than females (Thompson and Munro, 1978; Sadovy and Colin, 1995). In heavily exploited areas of Puerto Rico, Florida (Figs. 22 and 23) and Cuba (Espinosa, 1980), most catches consisted of juveniles.

Individuals tend to be smaller inshore (more heavily exploited areas) than offshore (less exploited areas). In Bermuda and Jamaica (Figs. 24 and 25), and off the U.S. Atlantic coast, smaller Nassaus are found on shallow reefs, with larger individuals on deep reefs (SAFMC[24]).

Epinephelus itajara The maximum length for jewfish ranges from 2,000–2,500 mm TL (Heemstra and Randall, 1993) with a maximum weight of 320 kg (Smith, 1971). Individuals of more than 225 kg have been commonly reported throughout the jewfish's range and the International Game Fish Association all-tackle record (as of 1990) is 308.44 kg (Heemstra, 1991). Male and female size ranges overlapped in the eastern Gulf of Mexico (Bullock et al., 1992). Of 481 fish sampled, mainly by speargun and handline, sizes ranged from 795–2,057 mm TL for males, 338–2,155 for females, and 75–2,160 for fish of undetermined sex (Bullock et al., 1992).

The great majority of jewfish taken commercially are immature (i.e. <1,200 mm TL). All 30 reported individuals caught in Puerto Rico between 1983 and 1993 were immature (i.e. less than 875 mm TL) (Caribbean Fishery Management Council [CFMC][25]). Between 1979 and 1987, the size range of jewfish from the U. S. Marine Recreational Fishery Statistical Survey intercept samples (n=21 fish) was between 250–1,570 mm TL, most less than 1,000 mm TL (GMFMC[9]).

4.2 Abundance and density

Epinephelus striatus The Nassau grouper was formerly one of the most common and important commercial groupers in the insular tropical western Atlantic and Caribbean (Smith, 1978; Randall, 1983; Appeldoorn et al., 1987; Sadovy, 1997). Declines in landings, catch per unit of effort (CPUE), and, by implication, abundance, have been reported throughout its range and it is now considered to be commercially extinct in a number of areas. Information on past and present abundance and density is based on a combination of anecdotal accounts,

[24] SAFMC. 1983. Fishery Management Plan, Regulatory Impact Review, and Final Environmental Impact Statement for the Snapper Grouper Fishery of the South Atlantic Region, 173 p.

[25] Caribbean Fishery Management Council (CFMC). 1993. Amendment 2 to the Fishery Management Plan for the Shallow-water Reef Fish Fishery of Puerto Rico and the U.S. Virgin Islands, 29 p.

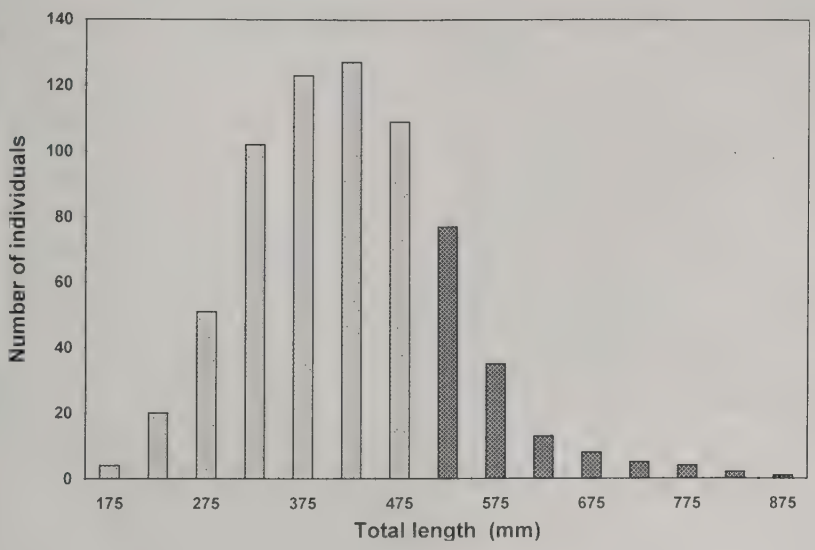

Figure 23

Length-frequency distributions of Nassau grouper, *Epinephelus striatus*, from recreational fishery landings between 1976 and 1985 in Biscayne National Park, Dade County, Florida (from Bohnsack, text footnote 31) (light stipple = immature; dark stipple = mature).

visual census surveys and fisheries data (see also Section 5.43).

Heavy fishing, especially of spawning aggregations, and certain fishing practices such as spearfishing and the excessive capture of juveniles in small-mesh fish traps, are almost certainly to blame for severe declines. With reports of illegal capture in the Atlantic and Caribbean, and legal capture continuing in other areas (e.g. U.S.V.I. territorial waters), an increase in Nassau grouper numbers is unlikely because the status of Nassau grouper has not changed noticeably since the ban on fishing for them in Caribbean and Atlantic waters was implemented (Section 6).

During the first U.S. survey of the fishery resources of Puerto Rico, the Nassau grouper was noted as a common and very important food fish, reaching a weight of 50 lbs (22.7 kg) or more (Evermann, 1900). By 1970, Nassau grouper was still the fourth most common shallow-water species landed in Puerto Rico (Thompson, 1978) and dominated the reef fish fishery of the Virgin Islands, where an aggregation in the 1970s contained an estimated 2,000–3,000 individuals (Olsen and LaPlace, 1979; CFMC[25, 26]). By 1981, however, the Nassau grouper had almost completely disappeared from catches in the U.S. Caribbean (CFMC[26]) and by 1986 was considered commercially extinct in the U. S. Virgin Islands/Puerto Rico region (Bohnsack et al.[27]). Only about 1,000 kg were landed during the latter half of the 1980s in Puerto Rico, most of them sexually immature (Sadovy, 1997).

Although management measures went into effect in the U. S. Caribbean in 1985, Nassau grouper numbers are not increasing, probably because illegal fishing persists (Beets[28]). Catches have plummeted in other areas where this species was once common, notably in Jamaica and possibly the Dominican Republic (Sadovy, 1997) (Section 5.43).

This species was once abundant in the Lesser and Greater Antilles. However, interviews with fishers, visual surveys, and analysis of commercial catches indicate that the Nassau grouper is no longer common in the Netherlands Antilles, probably as a result of intensive spearfishing during the

[26] CFMC. 1985. Fishery Management Plan, Final Environmental Impact Statement, and Draft Regulatory Impact Review, for the Shallow-water Reef Fish Fishery of Puerto Rico and the U.S. Virgin Islands. 104 p.

[27] Bohnsack, J. A., D. L. Sutherland, A. Brown, D. E. Harper, and D B. McClellan. 1986. An analysis of the Caribbean biostatistical database for 1985. Coast. Res. Dev. Rep. Carib. Fish. Mgt. Coun. Contr. No. CRD-86/87-10, 35 p.

[28] Beets, Jim. 1990. Division of Science and Mathematics, Jacksonville University, 2800 University Blvd North Jacksonville, FL 32211. Personal commun.

1960s and 1970s (Nagelkerken, 1982). Similarly, on the insular platform of Martinique, this species was clearly more abundant prior to the introduction of arrowhead fish traps, according to interviews with fishers (Gobert, 1994). Underwater visual censuses in St. Lucia, Jamaica, and the Dominican Republic produced no records of Nassau grouper (Roberts[29], Schmitt and Sullivan[30]) (Table 11).

In the western Atlantic, Nassau grouper have declined sharply in density, number, and average weight since 1975 (Bannerot et al., 1987). Density in Bermuda in the 1950s was estimated at 12 fish per acre (0.405 hectare), with the fish weighing an average of 1.1 kg (Bardach and Menzel, 1957); density and landings declined drastically between 1975 and 1981 (Luckhurst, 1996) such that the species is now considered commercially extinct (Sadovy, 1997).

Although there are few data on historic abundance of Nassaus off the U. S. mainland, it appears that abundance was once high in southern Florida (Springer and McErlean, 1962; Bohnsack[31]). Anecdotal reports from spearfishers noted large daily catches of Nassau in the 1950s (Bohnsack[31]). Starck (1968) reported Nassau grouper frequently at Alligator Reef in the Florida Keys. Recent interviews of Florida Keys' residents suggested that Nassaus were once caught in much greater numbers from the upper Florida Keys and the Bahamas. Reef fish surveys by the NMFS Southeast Fisheries Science Center's (SEFSC) Reef Team revealed low and declining densities from 1979–94 in southern Florida; of 3,518 visual point counts Nassau grouper were recorded 29 times, the number declining to zero in 1993 (Figs. 26A and B) (for census method, see Bohnsack and Bannerot, 1986). In the Dry Tortugas, where Nassaus were once abundant, only one individual was recorded in 1994 out of 183 point censuses and none in 37 predator censuses. On Elbow Reef, Florida Keys, mean Nassau densities were 0.01–0.04 fish per 100 m^2 in 1993–94 (Sluka et al., 1998), with few seen on census dives through the Florida Keys (Table 11). Censuses comparing areas protected and unprotected from fishing indicate that Nassau grouper, where protected, have a higher density and were one of the dominant grouper species observed (Sluka et al., 1994).

Most alarming, however, have been declines in numbers of Nassau grouper aggregating to reproduce at spawning sites (Sadovy, 1993, 1997). In many locations, aggregations are heavily targeted and between about one quarter and one half of all known aggregations no longer form at traditional sites (Section 5.43). The impact of aggregation losses on reproductive output and population abundances is not known, but is likely to be substantial. For example, in both Bermuda and Puerto Rico, where traditionally fished aggregations no longer form, local stocks are considered to be commercially extinct. Population abundances are expected to be largely dependent on the supply of recruits from healthy spawning aggregations.

Epinephelus itajara The decline in inshore jewfish populations began in the 1950s or 1960s, undoubtedly

[29] Roberts, Callum. 1994. University of York, York Y01 5DD, UK. Personal commun.

[30] Schmitt, E. F., and K. M. Sullivan. 1994. Research applications of volunteer generated coral reef fish surveys. The Nature Conservancy and the University of Miami, Department of Biology Report. Coral Gables, Florida. 38 p.

[31] Bohnsack, J. A. 1990. Black and Nassau grouper fishery trends. Appendix in South Atlantic Reeffish Plan Development Team Report of the Snapper-Grouper Assessment of the South Atlantic Fishery Management Council, 18 p.

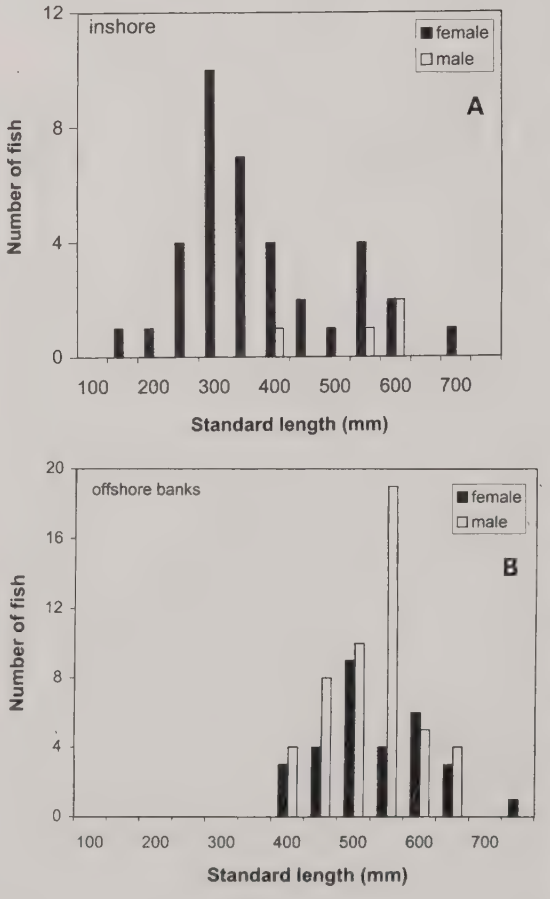

Figure 24
Length distributions of Nassau grouper, *Epinephelus striatus*, in Bermuda from (A) inshore and (B) offshore areas (from Bardach et al., 1958).

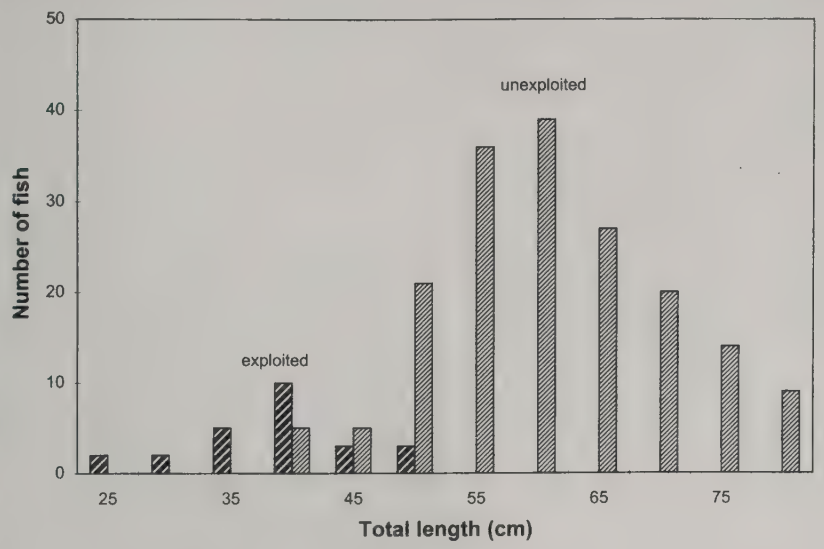

Figure 25
Length distributions of Nassau grouper, *Epinephelus striatus*, in Jamaica from inshore exploited areas (darkly shaded) (n=20) and offshore unexploited (lightly shaded) areas (n=163) (from Thompson and Munro, 1978).

Table 11
Number and percentage of dives at each location in the Florida Keys and the Caribbean where Nassau grouper and jewfish were observed during volunteer censuses conducted by R.E.E.F., the Reef Environmental Education Foundation. All censuses were conducted in 1994. Data from Schmitt and Sullivan (text footnote 30).

Location	Number of dives	Minutes of bottom time	Dives with one Nassau observed	Dives with 2-10 Nassau observed	Percent of dives with Nassau observed	Dives with one jewfish observed	Dives with 2-10 jewfish observed	Percent of dives with jewfish observed
Key Largo	145	10,449	14	5	13	0	0	0
Marquesas Keys	18	1,307	3	1	22	0	0	0
Key West	158	9,910	5	0	4	0	0	0
Dry Tortugas	204	11,517	13	5	9	2	0	1
Dominican Republic	70	4,165	0	0	0	0	0	0

a consequence of intensive fishing of aggregations and spearfishing of adults which are unwary of divers. Once common in Florida and parts of the Gulf of Mexico, the jewfish is rarely seen nowadays in these areas or, indeed, elsewhere in the West Indies (Randall, 1983). It is uncommon in the Netherlands Antilles following depletion by spearfishing (Nagelkerken, 1981). Although the historical center of abundance was peninsular Florida, the fishery there closed in 1990 due to rapid declines in catch and CPUE (Section 5.43) and in the mid-1990s, individuals were rarely seen. For example, one diver in Palm Beach County who dives approximately 100–150 times a year has seen but one jewfish since 1990 and noted that where an aggregation of jewfish once formed 19 km offshore from Vero Beach in 22–24 m of water, only 1 or 2 fish were observed in recent years. Whereas video footage of aggregations off Palm Beach and Jupiter, Florida, in 1959 and in 1969 shows groups of several dozen jewfish in shallow reef areas (Parks[32]), no aggre-

[32] Parks, William. 1992. 919 S.W. 27th Place, Boynton Beach, FL 33435. Personal commun.

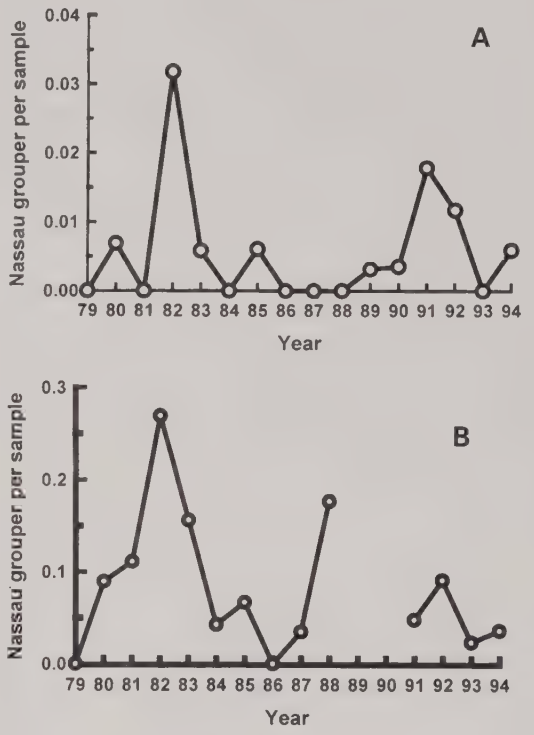

Figure 26
Number of Nassau grouper, *Epinephelus striatus*, observed from Biscayne National Park to the Dry Tortugas in the Florida Keys: (A) per sample of 5 minute visual point censuses; and (B) per 15 minute predator count. (NMFS Southeast Fisheries Science Center's Reef Resources Team).

gations have been observed off the east coast of Florida within the last 25 years. The jewfish was reportedly common 10 to 20 years ago off Belize and is now rarely seen (Wells[33]). A survey conducted in 1994 on the status of the jewfish along the coast of Brazil showed that this species had become rare, with a drastic decline in abundance over the previous 10 years, possibly due to illegal spearfishing with SCUBA. Increased numbers, however, were recently observed at Fernando de Noronha in a marine park protected since the early 1980s (Ferreira Padovani and Maida, 1995).

Exploitation of deep-water jewfish populations had barely started when declines were noted. Heavy exploitation of offshore populations was initially limited by the absence of electronic navigation equipment, although large jewfish (170–200 kg) were taken from Louisiana oil platforms in the 1960s (Cuccia 1962, 1963). When the LORAN-C navigation device became widely available in the 1980s, the isolated reefs and wrecks offshore became easy to locate repeatedly and rapid declines in jewfish catches resulted (Eklund[34]).

The number of jewfish on each of four aggregation sites in the eastern Gulf of Mexico declined shortly after discovery. On deep water wrecks, known aggregations of up to 100–150 jewfish declined to 0–10 fish by 1989 (DeMaria[17]) (Fig. 27); since early estimates of numbers in the low visibility waters were probably conservative, the decline in abundance is likely even greater than these numbers suggest.

Visual censuses produce few jewfish sightings. There were no observations of jewfish in any of the NMFS SEFSC Reef Team visual point counts or predator searches, from 1979–94, from Biscayne National Park to the Dry Tortugas, Florida, off the Florida Keys (SEFSC[35]). Jewfish were seen on only two of the 204 Reef Environmental Education Foundation (R.E.E.F.) dives logged in the Dry Tortugas, Florida, with none at the other R.E.E.F. census locations (Table 11).

4.3 Nâtality and recruitment

4.31 Reproduction rates

Epinephelus striatus Fecundity estimates from wild-caught Nassau grouper are few and varied, but suggest a mean relative fecundity of between 3 and 5 eggs/mg of ripe ovary, depending on the method used, i.e. which stages of oocytes are included in egg counts. Estimates from Belize yielded a mean relative fecundity of 4.1 eggs/mg ovary weight and a mean total number of oocytes (stage unspecified) of 4,200,000 (range = 350,000–6,500,000 for females of 300–700 mm SL) (Carter et al., 1994). Estimated number of eggs in the ripe ovary (90.7 g) of a 445 mm SL individual from Bermuda was 785,101 (Bardach et al., 1958). In the Virgin Islands, fecundity estimates made from 42 mature females gave a mean value of 4.97 eggs/mg of ovary (s.d.=2.32) with mean egg production of 4,800,000 eggs (Olsen and LaPlace, 1979). However, since this latter estimate includes previtellogenic oocytes, which may not recruit into the vitellogenic stock prior to spawning, it is considered to be an overestimate. Fecundity estimates were also made, based on vitellogenic oocytes only, from Bahamas fish (Fig. 28) producing a mean relative fecundity of 2.9/mg

[33] Wells, Sue. 1993. 56 Oxford Road, Cambridge CB4 3PW, UK. Personal commun.

[34] Eklund, A. M. 1994. Status of the stocks of Nassau grouper, *Epinephelus striatus*, and jewfish, *Epinephelus itajara*. Final Report. SEFSC report. Miami Contribution #MIA-94/95-15, Miami, FL, 170 p.

[35] SEFSC, NMFS, NOAA, 75 Virginia Beach Drive, Miami FL 33149. Unpubl. data.

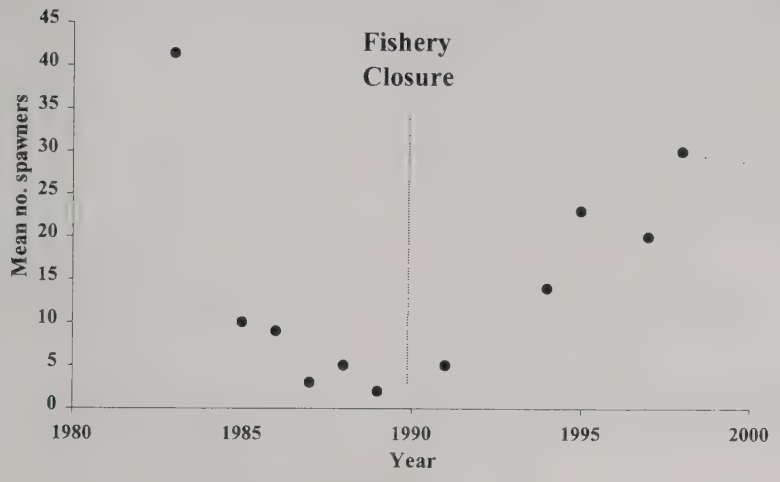

Figure 27
Estimated mean number of jewfish, *Epinephelus itajara*, observed on wrecks in the Gulf of Mexico in 30–50 m of water before and after fishery closure in 1990. Data are taken from the log of Don DeMaria[17].

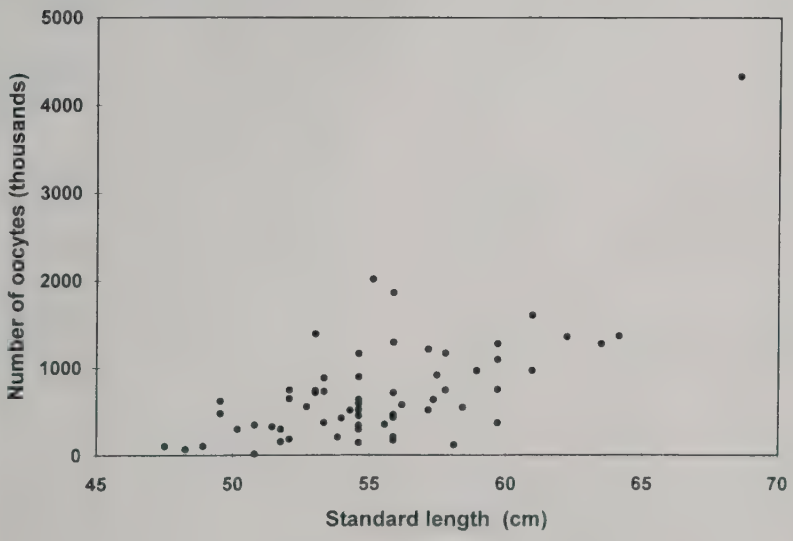

Figure 28
Relationship between number of vitellogenic oocytes (>0.17 mm diameter) and standard length in Nassau grouper, *Epinephelus striatus*, from the Bahamas. The regression line is: No. oocytes = –5407734.1 + 110905.9 SL (r^2 = 0.44; $p<0.001$; n=64). Counts were taken on ovaries collected several days prior to and on the day of the full moon in December 1988 and January 1989. [Figure prepared by Pat Colin, Yvonne Sadovy, and Ione Hunt von Herbing as part of a project supported by the Caribbean Marine Research Center, National Undersea Research Program, NOAA; P. Colin–project leader].

ripe ovary (s.d.=1.09; n=64) and a mean fecundity of 716,664 (range = 11,724–4,327,440 for females of 475–686 mm SL). Estimates of oocyte production from animals induced to spawn in captivity are closer to those based solely on vitellogenic oocyte counts and are given in Section 7. In the absence of more precise fecundity and annual spawning frequency data, annual fecundity should be considered to fall towards the lower end of the above estimates.

Epinephelus itajara The only indication of egg output comes from batch fecundity estimates made for two females. The first measured 1,322 mm SL and had a batch fecundity of 38,922,168 ± 1,518,283 oocytes. The second measured 1,397 mm SL and had a batch fecundity of 56,599,306 ± 1,866,130 oocytes (Bullock and Smith, 1991).

4.32 Factors affecting reproduction

Epinephelus striatus All reproductive activity is thought to take place during brief annual spawning aggregations of hundreds to thousands of individuals, although it is possible that spawning may occasionally occur outside of aggregations, on occasion (Sadovy and Colin, 1995). Given that many of the spawning aggregations have become severely depleted and between 25–50% no longer form, it is probable that reproductive potential for some populations has been seriously compromised. Moreover, observations of reproductive activity, duration of aggregations, and intensity of color changes suggest that spawning becomes abbreviated or ceases when fish numbers are low (Section 3.16) (Colin, 1992; Aguilar-Perera and Aguilar-Dávila, 1996). In extreme cases, such as Bermuda, or Puerto Rico, where aggregations no longer form, Nassau grouper are now rarely taken or observed.

The loss of juveniles in capture fisheries (Section 5.42), or through loss of critical juvenile habitat, will almost certainly influence numbers of reproductive adults, with potential negative impacts on reproductive output.

Epinephelus itajara Factors affecting reproduction in the jewfish are not known. The size of spawning populations is likely influenced by loss of reproductive adults, especially from fished aggregations, sportfishing of large individuals, removal of juveniles in commercial and recreational catches (Section 5.42), and loss of critical juvenile habitat.

4.33 Recruitment

Epinephelus striatus Data on recruitment of larvae onto reefs suggest that their onshore transport relies heavily on cross-shelf winds and currents and occurs in short pulses during highly limited periods each year (Shenker et al., 1993). Recruitment of Nassau larvae occurs at an average 32 mm TL (Eggleston, 1995) and was monitored for a 75-day period from mid-December through February using channel nets suspended in tidal passes between islands on the edge of the Exuma Sound, Bahamas. Assuming that the full recruitment window was sampled, 86% of the total annual recruitment of Nassaus occurred in this area during a single 4-day storm, while another 10% recruited during a second storm event. During this sampling period, 13% of all larvae sampled were Nassau grouper which recruited during particularly short, discrete pulses when compared to other taxa taken throughout the study. While early recruitment occurs into both macroalgae and seagrass beds, subsequently higher abundances in macroalgae are probably due to a combination of active substrate selection behavior for macroalgae and high post-settlement predation in seagrass (Nadeau and Eggleston, 1996) (Section 2.21).

Data on recruitment into the fishery indicate that age and size first susceptible to capture are 4–7 years and 275+ mm TL, respectively (Table 3). In some areas, most of the catch is composed of juveniles (e.g. Puerto Rico and Cuba). Olsen and LaPlace (1979) calculated age of first capture at 4–5 years, although immature fish of 2 years (< 300 mm TL) were also recruited. Mean size of recruitment into the fishery in Jamaica was estimated at 570 mm TL (about 5 years) on oceanic banks for handline and fish trap fisheries; the minimum length captured was 275 mm TL and the full retention length was 625 mm TL (Thompson and Munro, 1978). Modal ages reported for a Cayman Islands aggregation and a stock in Cuba were 6–8 years (Claro et al., 1990; Bush et al., 1996), suggesting that individuals were not fully recruited until this age range.

Epinephelus itajara Size of settlement out of the plankton is not known, although a larva close to settlement was taken at a little over 20 mm TL in a mangrove in Puerto Rico (Dennis et al., 1991). Jewfish are often recruited into the fishery when still immature, i.e. at 500 mm TL and above (once minimum size limits of 500 mm TL were introduced) (Table 3). Individuals enter the breeding population at 1,000–1,350 mm TL, based on catches from aggregations in the eastern Gulf of Mexico (Bullock et al., 1992).

4.4 Mortality and morbidity

4.41 Mortality rates

Epinephelus striatus Estimates of natural mortality (M), based on length-frequency data from Nassau grouper taken on unexploited banks in Jamaica, ranged from

0.17 to 0.30 (Thompson and Munro, 1978). Total mortality (Z), using length frequency data, was estimated at 0.55 in Cuba. With a low natural mortality (M) determined to be 0.18, this indicates high fishing mortality (F) of 0.37 (Baisre and Páez, 1981).

Epinephelus itajara Natural mortality (M) of jewfish is assumed to be 0.15, extrapolating from data on other grouper species (GMFMC[9]). Total mortality (Z) of jewfish in the Gulf of Mexico was estimated from the age distribution as 0.85 for fish greater than 11 years (GMFMC[9]). These results indicate a low natural mortality and a high fishing mortality (F) of 0.70.

4.42 Factors affecting mortality

Epinephelus striatus The only known causes of natural mortality in the Nassau grouper are predation by barracuda, shark, and conspecifics (Section 3.34) and severe declines in seawater temperature. Sharks were observed attacking Nassau groupers in spawning aggregations (Olsen and LaPlace, 1979) and dead Nassau grouper were reported after a cold spell of 11–14°C in Florida (Bohnsack, 1983).

Epinephelus itajara There is little information about natural mortality of jewfish. Gilmore et al. (1978) note that this species suffers mortality after a cold spell (13°C). Juveniles of both species are probably prey to other carnivorous fishes such as groupers, snappers, sharks, barracudas. and moray eels (SAFMC[24]).

4.5 Dynamics of populations

Epinephelus striatus* and *Epinephelus itajara Little is known about the dynamics of unexploited stocks of Nassau grouper and jewfish. Limited information on their growth rates, mortality, and recruitment is available (Sections 3.43, 4.33, and 4.41). Spawning stock biomass per recruit has not been quantified for either species but landings data clearly show a chronological trend from abundance to rarity in many areas (e.g. CFMC[25]; Sadovy, 1997). Of particular concern has been the rapid and extreme decline in numbers taken from traditional aggregation sites. In general, slow-growing, long-lived species with limited spawning periods and, possibly, with only a narrow recruitment window (Section 4.33) are susceptible to overexploitation (Bannerot et al., 1987; Polovina and Ralston, 1987; Bohnsack[1]). Such characteristics appear to typify the Nassau grouper and, to a large extent, the jewfish.

High fishing mortality can annihilate aggregations (Bohnsack[1]); since groupers at spawning sites are highly concentrated and are said to be less cautious, they are therefore more likely to be caught than at other times. How important spawning aggregations are to reproductive success has not been quantified but a substantial proportion of, if not all, annual spawning occurs in aggregations. The extent to which fishing at aggregation sites disrupts spawning behavior is likewise unknown, but is probably significant (Section 3.16) (Bannerot et al., 1987). Moreover, to what extent local recruitment depends on spawning activity at local aggregations, or on that occurring upstream, is unknown, making management and conservation decisions for declining stocks difficult.

Reef fish may be recruitment-limited (see Richards and Lindeman, 1987; Doherty and Williams, 1988). The threat of recruitment overfishing increases as reproductive adults decline, or if few juveniles survive to enter the adult population. Species such as these groupers, which produce pelagic eggs over limited time periods, may be subject to highly variable interannual recruitment success, making them particularly vulnerable to recruitment failure in poor years, or when population sizes are low.

The results of yield per recruit analyses for other groupers indicate that a large fraction of potential yield is taken at low levels of fishing mortality and that grouper stocks are unable to withstand anything other than light fishing pressure (Huntsman et al., 1983; Sadovy and Figuerola, 1992); this pattern is likely to also apply to the Nassau grouper and the jewfish. Since the maximum biomass of a cohort is attained at older ages, maximum sustainable yield or maximum yield per recruit is only reached at low capture levels and when only large fish are landed (Alverson and Carney, 1975, cited in Bullock et al., 1992). Moreover, with increase in fecundity with body weight, the stocks' reproductive potential declines markedly when older, larger fish are selectively captured.

4.6 The population in the community and the ecosystem

Epinephelus striatus The Nassau grouper, because of its former abundance in certain areas, may be a key predator in the ecosystem. This species takes many types and sizes of food and moves among different habitats, such as seagrass beds and coral reefs, at different life-history stages or reproductive phases, or while hunting. Given its former abundance in some areas, its depletion could impact the reef community.

Epinephelus itajara The jewfish is the largest American grouper and one of the two biggest grouper species worldwide. Due to its large size and reported food habits, this sedentary and site-specific species is likely to have an impact on its home reef invertebrate and small fish populations, although removal of a reef's resident jew-

fish has unknown effects on the food web structure and local prey densities. The role that juvenile jewfish play in mangrove habitats is likewise unknown.

Jewfish sightings are being used as criteria for success in the restoration of the Southern Florida ecosystem (Southern Florida Management and Coordination Working Group[36]) based on the fact that, historically, this species was an abundant predator along the Everglades' Ten Thousand Islands region.

5 EXPLOITATION

5.1 Fishing equipment

Epinephelus striatus Nassau grouper are fished commercially and recreationally by handline, longline, fish traps, spearguns, and gillnets. Aggregations are mainly exploited by handlines, or by fish traps, although gillnets are now used in Mexico. Preferred gears vary regionally and patterns of gear use are best summarized geographically. In general, traps are used most intensively in insular areas. Recreational fishing with handline is particularly important off Florida.

Bahamas and Caribbean In the Bahamas, handlines, traps, and spearguns (the latter used with hookah in recent years) take Nassau grouper (Sadovy, 1997) (Section 5.43). In the U.S. Virgin Islands and Puerto Rico, reef fish are caught by fish trap with some spearfishing and handlining (Bolden[37]). The boats in this fishery are small, less than 7.9 m long (Appeldoorn and Myers, 1993; CFMC[25]). Juvenile Nassau grouper are readily retained in traps since the mesh size is typically too small (between 44–51 mm) for most to escape.

In the Lesser Antilles, most larger groupers are fished with handline and with traps from 4–8 m long boats equipped with 8 to 48-horsepower outboard engines (Mahon, 1990); since the shelf is so narrow off the Lesser Antillean Islands, there has been no great need for larger boats. Groupers are sometimes caught off the deeper slopes using electric reels or mechanized winches for hauling traps (Mahon, 1990).

Off Cuba, Jamaica, and Hispaniola, trap fishing is the primary method for catching grouper (Munro and Thompson, 1983). Boats are typically non-mechanized and less than 6 m long (Claro et al., 1990; Baisre, 1993). The Antillean (arrowhead) fish traps are wooden-framed with galvanized wire mesh and one or two entrance funnels (Munro, 1983a). The single funnel "chevron traps" are commonly used in the eastern Caribbean, and the "S" or "Z" shaped traps, with dual entrance funnels, are found in Cuba and Jamaica. Most traps have mesh sizes between 25–50 mm (Munro, 1983a).

Central America In Mexico, handlines were used to catch groupers until the 1960s, when spearguns became more common. The efficiency of spearguns led to a decline in annual landings (Aguilar-Perera, 1994). After spearguns were banned, gillnets were used as barrier nets around aggregation sites. Mean size for gillnet (20.3 cm mesh) catches at two aggregations sites was about 600 mm TL (Sosa-Cordero and Cárdenas-Vidal, 1997). In Quintana Roo state, Mexico's fishers are known to capture grouper by tying a live female to a line, pulling her up rapidly, and netting the males that follow her to the surface.

In Belize the speargun and handlines have been used to fish grouper aggregations since at least the 1940s (Thompson, 1945; Perkins, 1983), with fish traps increasing after 1986 (Auil[16]). The fishing boats of Belize comprise either 5–7 m vessels equipped with outboard engines or larger sail-powered boats (Perkins, 1983). Handlines are often rigged with 3 to 15 hooks per line (Munro, 1983a).

Florida In the eastern Gulf of Mexico, handlines and longlines accounted for 80–100% of Nassau grouper commercially landed, by weight, from 1986–92 (Table 12). Incidental catch of Nassau grouper occurred from fish traps, with the number of trap-caught groupers increasing since 1984 (GMFMC[38]). In the 1990s, most catch from the recreational fishery was from private/rental boats (Table 13).

Off Florida's Atlantic coast, Nassau grouper were caught primarily by handlines (Table 12), although catches from spearfishing took more than one quarter of the commercial landings in 1989, 1991, and 1992. Data prior to 1986 are unavailable because grouper were not reported by species prior to that year. Most recreational catch in the U.S. Atlantic came from private/rental boats (Table 13).

Epinephelus itajara In the Gulf of Mexico and the Atlantic, U.S. commercial capture of jewfish was mainly from handline and speargun, with bycatch from longlines and trawl fisheries (GMFMC[9]) (Table 14). The directed fishery for jewfish primarily depended on spearfishing; the percentage of jewfish landed through spearfishing increased substantially after 1984 in the Gulf and increased between 1988–89 in the Atlantic; from

[36] Science Sub-group of the Southern Florida Management and Coordination Working Group. 1993. Federal objectives for Southern Florida Restoration. Draft report. 71 p.

[37] Bolden, S. K. 1994. A summary of biological and fishery data on red hind (*Epinephelus guttatus*) and coney (*Cephalopholis fulva*) stocks in the U.S. Virgin Islands. NOAA/NMFS Miami Laboratory Contrib. No. 93/94–32, 33 p.

[38] GMFMC. 1989. Amendment Number 1 to the Fishery Management Plan for the Reef Fish Fishery of the Gulf of Mexico. Tampa, Florida. 356 p.

Table 12

Percent commercial landings of Nassau grouper by gear type for the Atlantic and Gulf of Mexico coasts of Florida from 1986-92. Nets include drift nets, gillnets, and run-around nets; handlines include electric and hydraulic reels, as well as bandit rigs. Longlines are bottom reeffish longlines. Data from NFMS General Canvass Landings System. [Note that these landings are all from Florida.]

	1986	1987	1988	1989	1990	1991	1992
Atlantic coast							
Fish traps	0	0	0	5.81	0	1.6	0
Nets	0	0	0	0	0	1.86	0
Handlines	100	0	54.81	68.49	100	70.8	68.7
Longlines	0	0	45.19	0	0	0	0
Spearguns	0	0	0	25.7	0	25.75	31.3
Total landings (lbs)	9,476	0	582	1,498	3,289	3,072	3,447
Gulf of Mexico coast							
Fish traps	13.8	0	0.56	0	4.07	4.19	1.09
Nets	0	0	0	0	0	0	0
Handlines	79.31	0	23.37	38.2	91.08	46.8	98.91
Longlines	0	0	76.06	61.8	4.85	49.01	0
Spearguns	6.89	0	0	0	0	0	0
Total landing (lbs)	5,804	0	3,722	4,283	3,364	2,628	6,065

Table 13

Percentage distribution by boat type of Nassau grouper caught in the U.S. recreational fishery in the Atlantic Ocean and in the Gulf of Mexico (all states). Fish caught include those reported released alive or dead. Data are from the Marine Recreational Fishery Statistical Survey, the NMFS headboat catch estimates, and the Texas Parks and Wildlife estimates. The shore fishing category was not measured in Texas after 1985.

	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
Atlantic catch															
Shore fishing	0	0	37.87	4.11	0	0	0	0	0	0	23.60	0	0	0	0
Private/rental boats	98.72	100	52.36	88.96	70.99	86.70	64.19	99.37	99.62	92.80	70.90	0	99.97	87.26	81.35
Headboats/ charter boats	1.28	0	9.77	6.93	29.01	13.30	35.81	0.62	0.38	7.20	5.51	100	0.03	12.74	18.65
Total number of fish	107,591	55,494	35,130	52,609	37,022	12,523	63,128	4,998	8,100	7,643	10,026	390	10,922	3,304	2,509
Gulf of Mexico catch															
Shore fishing	0	28.55	51.05	0	41.81	1.60	0.95	10.89	12.51	50.95	63.04	23.75	0	4.47	4.19
Private/rental boats	0	59.81	33.37	100	54.39	97.29	95.59	89.06	86.99	48.83	17.06	76.18	87.28	92.07	95.81
Headboats/ charter boats	100	11.64	15.58	0	3.80	1.11	3.47	0.05	0.50	0.22	19.91	0.07	12.72	3.45	0
Total number of fish	48,964	27,973	65,823	32,466	30,328	133,547	44,986	120,949	85,240	20,571	36,918	40,969	47,727	27,135	81,031

1986–88, handlines accounted for three quarters of the landings in the U.S. Atlantic jewfish fishery.

The U. S. recreational fishery, characterized by private and rental boats (Table 15), primarily used spearguns (GMFMC[9]). Recreational fishers, using handlines, mostly took small fish because jewfish are difficult to land at larger sizes (SAFMC[24]). In the Gulf of Mexico, the recreational sector took substantially more jewfish than the commercial sector. The U.S. recreational and commercial fisheries for jewfish were considerably smaller in the Atlantic than in the Gulf of Mexico (Tables 14 and 15).

In the Caribbean, jewfish are mainly caught by spearfishing; their large size, lack of wariness towards divers, and their sluggish ways make them susceptible to the spear (CFMC[25]). Juvenile jewfish are caught in traps (CFMC[25]).

Table 14

Percent commercial landings of jewfish by gear type for the Atlantic and Gulf of Mexico coasts of Florida. Handlines include electric and hydraulic reels and bandit rigs. Longlines are bottom reeffish longlines. Data from 1979–85 for the west coast of Florida are from the Gulf of Mexico Reef Fish Fishery Management Plan, Amendment 2, 1990. Data from 1986-90 are from the NMFS General Canvass and Accumulated Landings System. [Note that these landings are all from Florida]. No data for Atlantic 1979–85.

	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Atlantic coast												
Shrimp trawls								0	0	0	0	9.65
Handlines								74.33	100	78.52	37.89	32.69
Longlines								0	0	0	0	0
Spearguns								25.67	0	21.48	62.11	57.66
Total landings (lbs)								10,492	17,911	12,931	8,669	1,814
Gulf of Mexico coast												
Shrimp trawls	7.3	1.1	1.3	0.8	1.0	0.7	0.1	1.81	1.68	1.99	2.68	0
Handlines	87.2	87.8	81.1	69.8	64.4	67.6	39.7	40.07	39.12	29.13	41.14	75.29
Longlines	0	7.1	11.2	21.1	26.2	20.7	31.4	19.84	14.56	9.87	8.39	8.92
Spearguns	5.4	4.1	6.4	8.3	8.4	11.1	28.8	38.28	44.64	59.00	47.80	15.79
Total landings (lbs)	34,107	41,591	54,950	49,894	68,615	70,374	107,355	108,952	99,951	135,715	93,066	7,488

Table 15

Percentage distribution by boat type of jewfish caught in the U.S. recreational fishery in the Atlantic Ocean and in the Gulf of Mexico (all states). Fish caught include those reported released alive or dead. Data are from the Marine Recreational Fishery Statistical Survey, the NMFS headboat catch estimates, and the Texas Parks and Wildlife estimates. The shore fishing category was not measured in Texas after 1985.

	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
Atlantic catch															
Shore fishing	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Private/ rental boats	0	100	100	0	0	100	0	0	96.89	99.51	0	0	100	0	0
Headboats/ charter boats	0	0	0	0	100	0	0	100	3.11	0.49	100	0	0	0	0
Total number of fish	0	6,884	995	0	262	6,492	0	1	932	821	610	0	1,163	0	0
Gulf of Mexico catch															
Shore fishing	22.08	0	0	0	0	35.11	0	0	0	0	53.85	0	95.50	71.36	0
Private/ rental boats	77.92	64.55	100	100	100	18.02	100	98.10	60.87	0	44.47	99.68	0	28.64	94.21
Headboats/ charter boats	0	35.45	0	0	0	46.87	0	1.90	39.13	100	1.71	0.32	4.50	0	5.79
Total number of fish	3,823	16,905	14,330	10,175	178	5,240	15,096	8,147	3,159	736	7,138	1,849	2,997	2,772	4,989

5.2 Fishing areas

5.21/5.22 General geographic distribution and range

Epinephelus striatus The center of exploitation of Nassau grouper is the Caribbean where it is taken at aggregations and as part of the multi-species, artesanal fisheries. Historically, the U.S. Virgin Islands and Puerto Rico's reef fisheries commonly took Nassau groupers at aggregation sites. Nassau grouper have also been caught from several sites off the Jamaican coast and off the northern coast of the Dominican Republic (Thompson and Munro, 1983; Sadovy, 1997). In Mexico, at least seven aggregation sites have been fished along the Yucatan Peninsula (Aguilar-Perera, 1994). One large aggregation site off Cay Glory, Belize, has been fished for many decades and other sites are known (Thompson, 1945). In Cuba, 21 aggregations were fished in the

Table 16

Percentage distribution by state of Nassau grouper caught in the U. S. recreational and commercial fisheries (all states). Recreational fish caught include those reported released alive or dead. Recreational data are from the Marine Recreational Fishery Statistical Survey, the NMFS headboat catch estimates, and the Texas Parks and Wildlife estimates. Commercial data are from NMFS accumulated landings files. TX = Texas; LA = Louisiana; MS = Mississippi; FL-W = Florida West; FL-E = Florida East; GA = Georgia; SC = South Carolina; NC = North Carolina; Atlantic coast: FL-E, GA, SC, and NC; Gulf of Mexico coast: TX, LA, MS, FL-W.

	1979	1980	1981	1982	1983	1984	1985	1986
Recreational landings								
TX	0.0	0.0	0.0	0.0	0.0	1.5	0.0	<0.1
LA	0.0	0.0	3.2	3.2	0.0	1.9	1.5	0.3
MS	0.0	0.0	0.0	0	0.0	<0.1	0.0	0.0
FL-W	31.3	33.5	65.2	35.0	45.0	88	40.1	95.7
FL-E	68.7	66.5	34.8	61.8	55.0	8.6	58.4	4
GA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total number	156,555	83,467	100,953	85,075	67,350	146,070	108,114	125,947

	1987	1988	1989	1990	1991	1992	1993
Recreational landings, continued							
TX	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LA	0.0	3.1	0.0	0.0	0.0	0.0	0.0
MS	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FL-W	91.7	69.8	78.6	99.1	81.4	89.1	97
FL-E	8.7	27.1	21.4	0.9	18.6	10.4	2.4
GA	0.0	0.0	0.0	0.0	0.0	0.5	0.5
SC	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
NC	0.0	0.0	0.0	0.0	0.0	0.0	<0.1
Total number	93,340	28,214	46,944	41,359	58,649	30,439	83,540

	1986	1987	1988	1989	1990	1991	1992	1993
Commercial landings								
TX	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0
LA	0.0	0.0	1.6	0.0	46.5	0.0	0.0	0.0
FL-W	37.1	0.0	78.6	70.4	27.1	46.1	69.8	63.3
FL-E	62.1	0.0	19.8	26.3	26.5	53.9	30.2	36.7
SC	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total landings (lbs)	15,633	0	4,737	6,080	12,432	5,700	11,428	7,416

last century; only one evidently remains and landings at that one are declining (Table 1).

In Atlantic waters, Nassaus are caught in the Florida Keys and the Bahamas (Bohnsack[31]). Over 20 spawning locations have been fished in Bahamian waters (Thompson[39]) (Table 1B), although the current status of many is unknown. Spawning sites are unknown off Florida.

In the Gulf of Mexico, Nassaus are caught primarily off southwest Florida, with much reported commercial and recreational catch from the southwest Florida Keys (Table 16, Florida-Gulf of Mexico). Both recreational and commercial catches of Nassau were higher from the Florida-Gulf of Mexico than from the Florida-Atlantic coast (Table 16). After 1991, these differences were probably partially due to fishery regulations banning all capture of Nassau groupers from the U.S. Atlantic waters, though not from the Gulf of Mexico; harvest is now banned in all U.S. waters.

Epinephelus itajara In the Caribbean, jewfish were caught in Kingston Harbor, Jamaica, in shallow waters (Thompson and Munro, 1983). Jewfish have also been observed in creeks, lagoons, and estuaries of Belize

[39] Thompson, Ronald. 1992. Department of Fisheries, P.O. Box N 3028, Nassau, Bahamas. Personal commun.

Table 17

Percentage distribution by state of jewfish caught in the U.S. recreational and commercial fisheries (all states). Recreational fish caught include those reported released alive or dead. Recreational data are from the Marine Recreational Fishery Statistical Survey, the NMFS headboat catch estimates, and the Texas Parks and Wildlife estimates. Commercial data from 1979–85 are from Gulf of Mexico Reeffish Fishery Management Plan, Amendment 2. Commercial data from 1986–93 are from NMFS General Canvass Landings files. Total commercial landings from 1979–85 do not include Atlantic catches. (See Table 16 for abbreviations.)

	1979	1980	1981	1982	1983	1984	1985		1986	1987	1988	1989	1990	1991	1992	1993
Recreational catch																
Texas	22.1	0	0	0	40.5	16.7	9.2		0.7	3.3	0.3	<0.1	0	0	0	0
Louisiana	0	6.8	0	13.8	0	20.9	0		87.1	1.6	0	0	0	0	0	0
Alabama	0	0	0	0	0	7.1	0		0	0	0	0	0	0	0	0
Florida–Gulf of Mexico	77.9	64.2	93.5	86.2	0	0	90.8		12.2	72.3	46.9	92.1	100	72.0	100	100
Florida–Atlantic	0	28.9	6.5	0	59.5	55.3	0		0	22.8	52.7	7.9	0	28.0	0	0
Total number of fish	3,823	23,789	15,325	10,175	262	11,732	15,096		8,148	4,091	1,557	7,748	1,849	4,160	2,772	4,989
	1979	1980	1981	1982	1983	1984	1985		1986	1987	1988	1989	1990	1991	1992	1993
Commercial catch																
AL,MS,LA, TX	7.3	6.5	9.9	22.0	17.3	9.3	10.9	TX	0.0	<0.1	0.3	0.1	2.0	0.0	0.0	0.0
								LA	0.2	1.0	1.8	0.0	19.2	100	0.0	0.0
								AL	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Florida–Gulf of Mexico	92.7	93.5	90.1	78.0	82.7	90.7	89.1	FL-W	90.6	84.0	88.9	91.4	63.4	0.0	0.0	0.0
								FL-E	8.7	15.0	8.5	8.6	15.4	0.0	0.0	0.0
								GA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100
								SC	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	0.0
Total landings (lbs)	36,797	44,478	61,012	63,995	82,942	77,614	120,531		120,317	119,032	152,726	101,868	11,807	798	0	16

(Thompson, 1945) but are not commonly taken elsewhere in the region.

Jewfish were seldom caught in the Atlantic, except offshore from Florida on reefs and wrecks (SAFMC[10, 24]). Few jewfish were taken between 1986 and 1993 in National Marine Fisheries Service commercial fishery surveys off Georgia or South Carolina (Table 17), although one individual was landed in the 1970s in Charleston, South Carolina (Keener-Chavis[40]).

In the Gulf of Mexico, jewfish were caught mainly in Florida, but also landed in Alabama, Louisiana, and Texas (GMFMC[9]) (Table 17). Until the closure of the jewfish fishery in 1990, the south Gulf counties of Florida (i.e. Monroe, Collier, Charlotte, and Lee) accounted for 78% of the total Gulf landings for jewfish, and all of Florida accounted for 99% of the Gulf jewfish landings (GMFMC[9]).

[40] Keener-Chavis, Paula. 1991. South Carolina Marine Resources Research Institute, PO Box 12559, SC 29412. Personal commun.

5.23 Depth ranges

Epinephelus striatus The depth range of the Nassau grouper is evidently dependent upon the distribution of natural reefs and hard substrate and, seasonally, on the location of spawning sites (Section 3.16). Off the Florida-Atlantic coast, commercial catches ranged from less than 3 nmi (5.6 km) from shore, to 12 nmi (22.2 km) offshore and beyond (Table 18). On the Florida-Gulf of Mexico coast, where hard-bottom areas extend farther offshore, >59% of the commercial landings between 1986 and 1992 were from more than 12 nmi (22.2 km) offshore (Table 18). In the U.S. Caribbean, on the other hand, where reefs are found up to a few feet from shore, most reef fish are caught inshore in territorial waters by small-scale fishers (Bolden[37]). Nassau grouper are taken in shallow shelf waters in the Lesser Antilles (Mahon, 1993) and at the shelf edge in 15–50 m off Cuba (Baisre, 1993) and Jamaica (Munro, 1983b). From a fishing survey of the Bahamas, Nassau grouper were common on shallow water banks and caught in waters less than 110 m deep (Thompson, 1978).

Table 18

Percent commercial landings of Nassau grouper by distance offshore for the Atlantic and Gulf of Mexico coasts of Florida from 1986–92. Distances are given in nautical miles (nmi). Data are from NMFS General Canvass Landings System.

Distance	1986	1987	1988	1989	1990	1991	1992
Atlantic coast							
< 3 nmi from shore	0	0	0	33.04	9.73	33.01	30.37
3–12 nmi from shore	92.55	0	74.05	17.96	8.06	14.52	14.85
12 nmi from shore or greater	7.45	0	25.95	49.00	82.21	52.47	54.77
Total landings	9,476	0	582	1,498	3,289	3,072	3,447
Gulf of Mexico coast							
< 3 nmi from shore	0	0	1.96	1.28	9.84	11.57	0
3–12 nmi from shore	14.21	0	1.93	6.70	31.03	9.44	4.34
12 nmi from shore or greater	85.79	0	96.10	92.01	59.13	79.00	95.66
Total landings	5,804	0	3,722	4,283	3,364	2,628	6,065

Table 19

Percent commercial landings of jewfish by distance offshore for the west and east coasts of Florida. Distance offshore is indicated in nautical miles (nmi). Data from 1979–85 for the west coast of Florida are from the Gulf of Mexico Reef Fish Fishery Management Plan, Amendment 2, 1990. Data from 1986–90 are from the NMFS accumulated landings and general canvass landings files. No data for Atlantic 1979–85.

Distance	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Atlantic coast												
< 3 nmi offshore								25.67	18.56	12.05	15.85	9.65
3–12 nmi offshore								0	5.16	45.23	16.18	56.23
12 nmi offshore or greater								74.33	76.28	42.72	67.97	34.12
Total landings (lbs)								10,492	17,911	12,931	8,669	1,814
Gulf of Mexico coast												
At the shore	0	0	0	0	0	0	0	0	0	0	0	5.4
< 3 nmi offshore	77.4	4.2	3.3	3.2	0.8	1.9	0.1	4.7	7.9	1.7	3.6	10.5
3–12 nmi offshore	8.3	3.6	6.7	4.1	12.0	16.4	9.8	9.7	14.2	14.3	16.5	7.0
12 nmi offshore or greater	14.4	92.1	90.0	92.8	87.2	81.7	90.2	85.6	77.9	84.0	79.9	77.0
Total landings (lbs)	34,107	41,591	54,950	49,894	68,615	70,374	107,355	108,952	99,951	135,715	93,066	7,488

Epinephelus itajara Jewfish are caught in shallow inshore areas, as well as on deep reefs and wrecks greater than 12 nmi (22.2 km) offshore (Table 19). A large percentage of the commercial landings are from offshore in the case of the Gulf of Mexico landings. As the number of jewfish observations by divers declined at known wrecks, some fishers suggested that jewfish occurred at greater abundance in waters deeper than 30–45 m (the practical limit for most diver-spearfishers). However, explorers of deeper areas in the Gulf of Mexico, using mixed gases that allowed them more time at depth, did not observe jewfish deeper than about 50 m (DeMaria[17]). In the Caribbean, jewfish have been caught and observed in shallow water, including Kingston Harbor, Jamaica (Thompson and Munro, 1983), and inshore off Belize (Thompson, 1945). Jewfish were included in the shallow inshore fishery of the Lesser Antilles (Mahon, 1993).

5.3 Fishing seasons

Epinephelus striatus There is geographic variation in the temporal concentration of fishing activity, but in many areas much fishing occurs during the reproductive season and spawning aggregations are heavily targeted (Section 5.43); in other areas, there is no apparent temporal association between catch volume and reproductive season. Commercial capture of Nassau grouper from U.S. Atlantic and Gulf of Mexico waters (1986–93), for example, does not reveal any concentration of commercial fishing during the reproductive period in the Atlantic (Fig. 29) and none at spawning aggregations. Elsewhere, however, up to 90% of total annual landings are taken during the reproductive season. In U.S. Atlantic waters, recreational catches peaked in the winter months, corresponding to the spawning season in the

nearby Bahamas (Fig. 30). Of the 1991 annual take of 400,000 kg of grouper (mainly Nassaus) landed in the Bahamas, 40% were taken during months of aggregation formation (Thompson[39]). In Cuba, landings data show that most annual catch is taken between December and January, the spawning season (Claro et al., 1990). Fishing for Nassau grouper off Belize and Mexico takes place mainly from late December through January or February, when spawning occurs, with 20–60% of Nassaus coming from aggregations in Mexico (Thompson, 1945; Craig, 1966; Aguilar-Perera, 1994; Aguilar[41]). Likewise, over 90% of annual landings come from spawning aggregations in the Cayman Islands (Bush[42]).

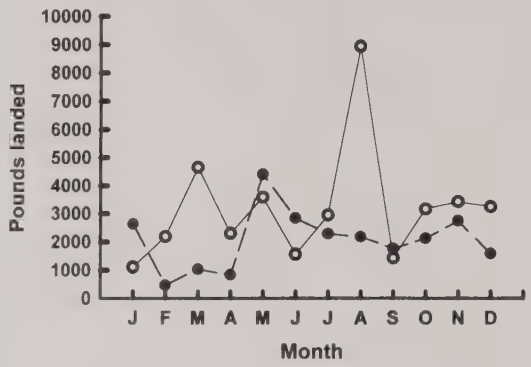

Figure 29
Pounds of Nassau grouper, *Epinephelus striatus*, landed by month from 1986–93 in the Gulf of Mexico (white circles) and the Atlantic (black circles) from the U.S. commercial fishery (NMFS General Canvass Landings System).

Epinephelus itajara There is geographic variation in the temporal concentration of fishing activity for the jewfish. Commercial and recreational landings from the Gulf of Mexico indicate that more jewfish were caught during the reproductive period with peak catches in August (Figs. 31A and 32) than at any other period, although care should be taken in interpreting these data since information on effort was not incorporated. Around Key West, Florida, adults were taken in greater

[41] Aguilar, Alfonso. 1992. Centro de Investigaciones de Quintana Roo, A. P. 424, C. P. 77000, Chetumal, Quintana Roo, Mexico. Personal commun.

[42] Bush, P. G. 1992. Protection and Conservation Unit, Department of the Environment, PO Box 486CT, Grand Cayman, British West Indies. Personal commun.

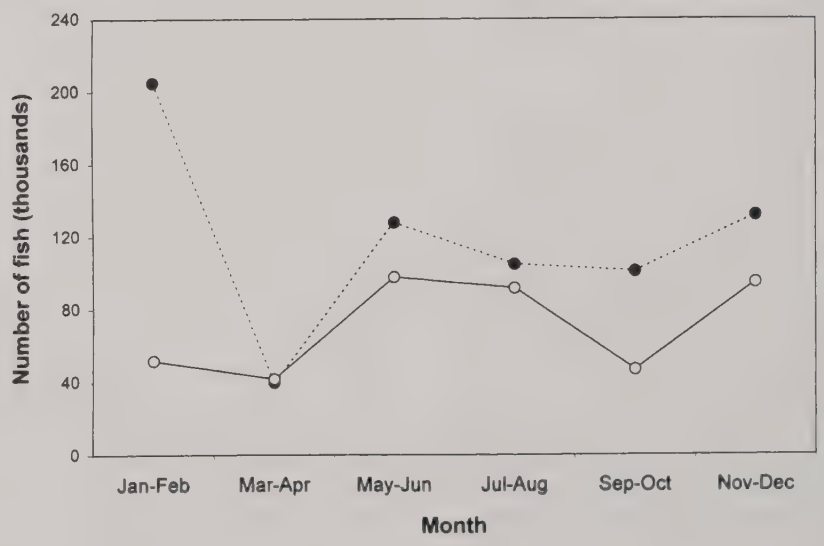

Figure 30
Number of Nassau grouper, *Epinephelus striatus*, caught seasonally (including catch-and-release) by the U.S. recreational fishery in the Gulf of Mexico (white circles) and the Atlantic (black circles) from 1979–93 (from the NMFS Marine Recreational Fisheries Statistical Survey, the NMFS headboat survey, and Texas Parks and Wildlife Department survey).

numbers by handline in July and August than at other times (Schroeder, 1924; Thompson, 1945). Similarly, in Belize, concentrated fishing for jewfish occurred in July-August around the full moon when they were known to aggregate, presumably to spawn (Thompson, 1945). In contrast to the Gulf of Mexico and Belize fisheries, Atlantic landings do not reflect any association between spawning season and catch rates (Fig. 31B). Recreational catch peaked in September-October from the Atlantic (Fig. 32); jewfish aggregations have not been reported in the Atlantic for many years.

5.4 Fishing operations and results

5.41 Fishing effort and intensity

Epinephelus striatus Fishing intensity has increased for many species of reef fishes over the last few decades, due partly to improved navigation and introduction of outboard motors, depth recorders, and power reels (SAFMC[24]). However, catch per unit effort (CPUE) is difficult to quantify for Nassau grouper, since there is no specific Nassau fishery outside of aggregation periods; instead, catches of this species are combined with those of other groupers and reef fishes. Quantification of effort is also confounded by the multiplicity of gears used, all with different fishing powers (Stevenson, 1981; Baisre, 1993). Moreover, in the Caribbean, the small-scale fishers land their fish at remote locations, making collection of reliable catch and effort data difficult (Stevenson, 1981).

Nassau grouper CPUE, calculated from headboats fishing off the Florida Keys (SAFMC[10]) and surveys in the Bahamas (Thompson, 1978) and Bermuda (Butler et al., 1993), is generally low or declining. Off the Florida Keys, from 1978–82, 0.07-0.17 fish were caught per trip, but this CPUE declined tenfold to 0.01-0.0 fish per trip from 1984–89 (SAFMC[10]). Elsewhere in southern Florida, CPUE was 0.01, or less, from 1983–89 (SAFMC[10]). Creel surveys from Biscayne National Park in southern Florida showed an almost ten-fold decline from 0.18 fish per trip in 1979 to less than 0.02 in 1987 (Bohnsack[31]). A fishing survey in the Bahamas from 1972–75 resulted in CPUE for Nassau grouper of 0.17 kg/reel hour in 55–110 m of water and 0.03 kg/reel hour in 110–165 m of water (Thompson, 1978). In Bermuda, the efficiency of grouper fishing declined from 1.8 kg of grouper per trap haul in 1975 to 0.65 kg in 1985 (Butler et al., 1993).

In the insular Caribbean, fishing pressure has increased substantially since the 1970s. In the U.S. Virgin Islands, the number of small boats increased three-fold at aggregation sites from 1968–76, with more than 1,000 kg of grouper caught per day. In the 1980s, 10–15 boats per day fished aggregations, using 6–15 traps per string and several strings deployed per boat (Beets and Friedlander, 1992); now aggregations no longer form. In the British Virgin Islands, fishing intensity has been much lighter and spawning aggregations still formed in the early 1990s, although their current status is unknown (Beets and Friedlander, 1992). In Jamaica, fishing surveys conducted in the early 1970s resulted in Nassau grouper CPUE of 1.4 kg per line hour in 20–30 m of water and 1.7 kg per line hour in 30–45 m (Munro, 1983b). With the advent of motorized boats and mechanized gears, intense exploitation led to lower catch rates of all reef fish and the disappearance of some species from multi-species catches (Stevenson, 1981). A survey of reef fishes in Jamaica in 1986 revealed no groupers (Koslow et al., 1988), and by 1989 Nassau grouper were rarely caught (Sadovy, 1997). In Cuba, the highest CPUE recorded at an aggregation was 15.7 kg/fisher sea day in 1977 (Espinosa, 1980).

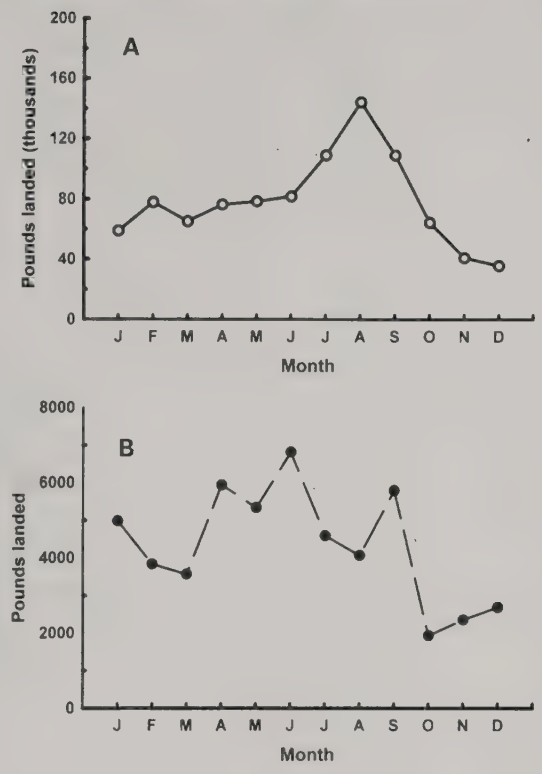

Figure 31
Number of pounds of jewfish, *Epinephelus itajara*, commercially landed by month (A) in the Gulf of Mexico from 1979–90 and (B) in the Atlantic from 1986–90. Data from 1979–85 are from Gulf of Mexico Fishery Management Council (1990); data from 1986–90 are from NMFS General Canvass Landings System.

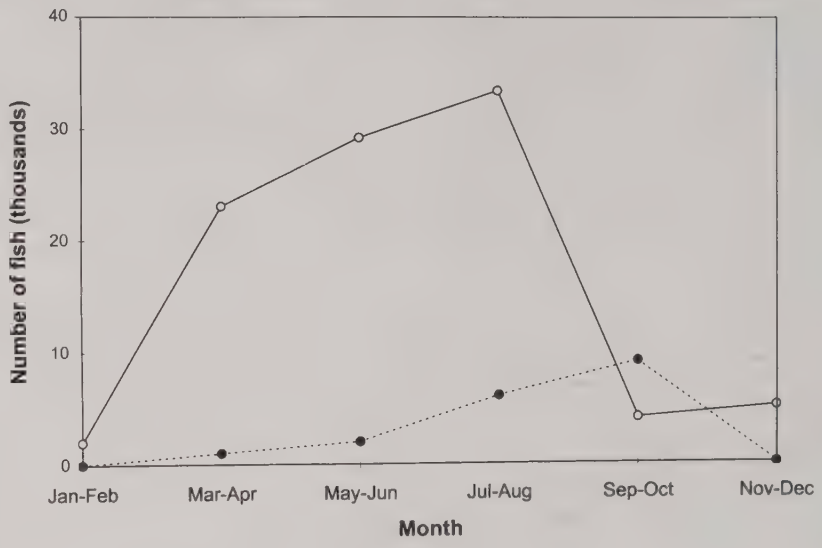

Figure 32
Number of jewfish, *Epinephelus itajara*, caught by season, including those caught and released, by the U.S. recreational fishery in the Gulf of Mexico (white circles) and the Atlantic (black circles) from 1979–93 (from the NMFS Marine Recreational Fisheries Statistical Survey, the NMFS headboat survey, and Texas Parks and Wildlife Department survey).

Off Belize, up until the 1960s, there was little fishing pressure on grouper stocks (Craig, 1966), but this has since increased markedly. Aggregations had been fished with low fishing effort since 1920 (Carter et al., 1994). From 1955–65, 250–300 boats would regularly fish an aggregation. By 1982, 1,200 fishers, representing 570 boats, were exploiting grouper spawning grounds (Perkins, 1983). The recreational fishing industry also increased because of increased tourism (Perkins, 1983).

In Mexico, at least one aggregation site off the Yucatan Peninsula had been fished since 1910–20. Landings of Nassau grouper declined in the late 1960s due to the introduction of spearguns at aggregation sites (Aguilar-Perera, 1994).

Epinephelus itajara Prior to the closure of the fishery in 1990, about 50 spearfishers targeted jewfish in the 1980s in the Atlantic (SAFMC[10]), while only two to three fished commercially for jewfish in the Gulf of Mexico. At one time, few commercial fishers directed any fishing effort to catching jewfish because they did not fetch the high price of snappers and other groupers (DeMaria[17]). The increase in value of jewfish, the availability of better electronic equipment, and the more widespread knowledge of the location of these fish caused an increase in overall fishing effort. U.S. commercial landings increased in the 1980s due to elevated demand and selling prices; the average price per pound of Gulf jewfish rose from 0.39 US$/lb in 1979 to 0.74 US$/lb in 1987. In Key West, the price of jewfish rose from 0.5–0.6 US$/lb in 1979 to 1.25 US$/lb in 1987 (GMFMC[9]). Since the 1980s, the widespread use of the navigational system LORAN-C increased precision in relocating productive fishing grounds, including isolated reefs. The LORAN-C numbers of several wrecks were published in books and in sport fishing magazines, increasing the likelihood that recreational and commercial fishers could locate these fish. The amount of time between intensive fishing and stock decline was short, suggesting that jewfish stocks are easily overexploited (DeMaria, 1996; Eklund[34]).

Surveys on effort or intensity of fishing on the jewfish showed that, off Jamaica in 1970–71, only one jewfish was caught out of 1,000 traps soaked for 16 days (Munro, 1983c). In Brazil, a preliminary survey carried out in 1994, based on questionnaries, indicated that jewfish numbers had declined drastically in the previous 10 years, probably due to spearfishing with SCUBA (Ferreira Padovani and Maida, 1995).

5.42 Selectivity

Epinephelus striatus* and *Epinephelus itajara Size selectivity for both species is highly variable and depends on

a combination of location, timing, and gear deployed. Fishing gears include fish traps, handline, and, to a lesser extent, speargun and gillnet. Table 3 summarizes ages and lengths at first capture (Section 4.33).

Many fisheries take large numbers of immature Nassau groupers because of locations fished and fishing gear characteristics. In Cuba and elsewhere, juveniles are selected because they are often found in shallower, inshore waters (e.g. Baisre, 1993). Caribbean fish traps typically have mesh sizes ranging from 25 to 50 mm which retain juveniles of these species (Munro, 1983a; CFMC[26]). In the U. S. Caribbean, at least 70% of Nassaus landed were within the immature size range (< 500 mm TL) (Fig. 22). Nassau grouper landed by handline at Biscayne National Park in southern Florida from 1976–85 were mostly immature (Fig. 23) (Bohnsack[31]).

Heavy selective pressure is also placed on mature spawning fish, since both species are particularly susceptible to capture from easily located spawning aggregations (GMFMC[9]) (Section 5.43) which are fished by traps, lines, and, in some areas, spears. Recently, gillnets (20.3 cm mesh) were used for the first time at two aggregation sites in Mexico taking individuals of 600 mm TL on average (Sosa-Cordero and Cárdenas-Vidal, 1997). The targeting of spawning aggregations results in high fishing mortality (Mahon, 1990) because fish are concentrated and catchability is high. This selective pressure is likely the primary cause for declines in, and apparent loss of, a number of well-known spawning aggregations of Nassau grouper and jewfish. While the genetic consequences of selectively removing many adults from specific sites are not known, there is reason for concern: in a study on the orange roughy, which also aggregates to spawn, loss of heterozygosity was significantly greater in those aggregations that were most heavily exploited (Smith et al., 1991).

5.43 Catches

Epinephelus striatus Both commercial and recreational catches of Nassau grouper declined throughout their range over the last 20 years, in some cases severely. In many areas up to 90% of annual commercial landings come from spawning aggregations. However, aggregations which were once productive now no longer form at several traditional sites in Belize, the Dominican Republic, Cuba, Honduras, Mexico, the Bahamas, Bermuda, Puerto Rico, and the U. S. Virgin Islands (Fig. 5). In those places where not one aggregation remains (e.g. Bermuda, Puerto Rico, U. S. Virgin Islands), commercial catches have declined so sharply that either local aggregations must supply a substantial proportion of the local stocks, or local fishing intensity is so high that few individuals survive to attain sexual maturity. Commercial catch exceeded recreational catch everywhere, except in Florida where the reverse was true.

Bahamas, Bermuda, and the Caribbean In the Bahamas, 70% of all grouper landed are Nassau grouper, which come from at least 23 exploited aggregations (Department of Fisheries, Government of the Bahamas) (Table 1b); about 800,000 lbs of Nassaus were landed in 1992 (Sluka et al., 1997a). While Nassau stocks were still in good condition in the early 1990s (Thompson[39]), loss or declines in aggregation catches have been noted. Forty percent of all groupers are caught between December and February, almost certainly at aggregations (Thompson[39]). However, several aggregations no longer form at traditional sites or have declined markedly in size. One site off Long Island, for example, fished since 1900, recently dropped from several thousand individuals to about 100 (Colin, 1992). An aggregation site at Andros Island (off High Cay), considered an important site by fishers in 1992 (Thompson[39]), was surveyed in 1998 and contained only scattered individuals at the expected spawning time (Ray[43]). In recent years, fishers have expanded their capture methods to include spearfishing with hookah at aggregation sites (Duncombe[44]).

In Bermuda, Nassau landings declined 15-fold between 1975–1981, from over 30,000 kg (74,000 lbs) to under 2,000 kg (4,000 lbs) (Fig. 33). The percentage of Nassau grouper in the total grouper catch declined from 16%, by weight, in 1975, to less than 1% of all grouper caught in 1989, a decline greater than for any other Bermuda grouper monitored (Bannerot et al., 1987; Butler et al., 1993; Sadovy, 1997). Although the annual catch of all groupers has recovered somewhat since 1981, that of the Nassau grouper has remained at a low of about 1,000 kg in 1984 (Butler et al., 1993; Ward[45]). Much of the annual catch came from aggregation sites which were fished until the mid-1970s, when they ceased to form (Sadovy, 1997); now Nassaus are rarely seen inshore.

Landings in the U.S. Caribbean have fallen sharply within the last three decades. Between 1966 and 1974, aggregation catches of more than 1,000 kg per day (approximately 300 fish and a significant proportion of the estimated 2,000–3,000 fish present at the site) were recorded from the U.S. Virgin Islands (Olsen and LaPlace, 1979). Between the aggregation seasons of 1974–75 and 1975–76, however, fishing pressure increased dramatically and total aggregation landings dropped threefold, from 14,460 kg to 4,930 kg, with a 76% decrease in CPUE (Olsen and LaPlace, 1979; Beets and Friedlander, 1992). By the 1980s, spawning aggregations once fished in St. Thomas and St. Croix no longer formed.

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[43] Ray, Carleton. 1998. Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903. Personal commun.

[44] Duncombe, Sam. 1992. P. O. Box SS 5905, Nassau, The Bahamas. Personal commun.

[45] Ward, Jack. 1992. Department of Agriculture, Fisheries and Parks, Flatts, Bermuda. Personal commun.

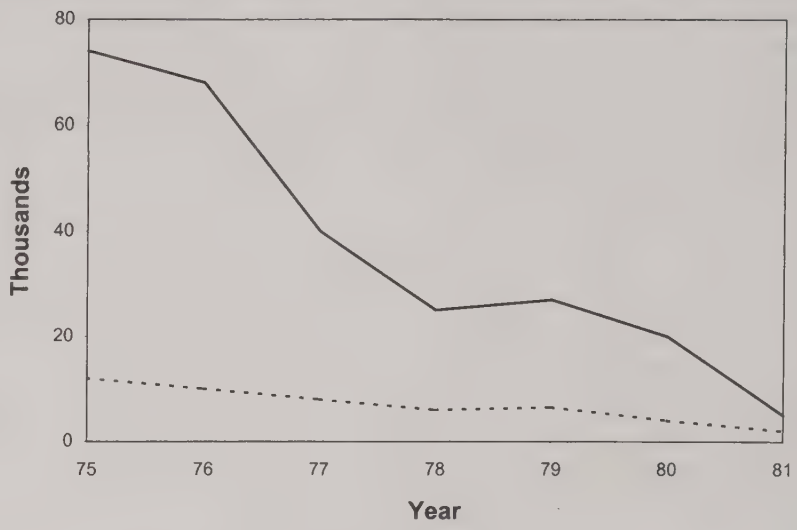

Figure 33
Commercial landings of Nassau grouper, *Epinephelus striatus*, by weight (solid line) (thousands of pounds) and number (dotted line) from 1975–81 in Bermuda (Bannerot et al., 1987).

Table 20
Landings in metric tons of Nassau grouper reported by the Food and Agriculture Organization of the United Nations (FAO, 1993). All other countries, besides Cuba and Colombia, did not report their catch by species.

Year	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Colombia	5	21	29	88	99	31	25	42	42	47
Cuba	409	377	341	403	262	332	262	263	159	151
Total	414	398	370	491	361	363	287	305	201	198

Early this century, the Nassau grouper was reported as the fourth most commonly landed shallow water species in Puerto Rico, yet none of the traditional aggregations persisted into the 1970s, and by the 1980s few individuals were taken. No data were available on Nassau grouper landings from the British Virgin Islands, although aggregations evidently still form (Beets and Friedlander, 1992).

Reported landings from Cuba show marked declines since the early 1960s (Table 20, Fig. 34). Nassau grouper constituted 7% of total annual landings in 1961–65, but less than 1.5% of the total landings in 1985–90 (Baisre, 1993; Claro[15]). Mean annual landings dropped three to four-fold between the early 1960s and late 1980s, despite increasing effort (Claro et al., 1990), with over 50% of annual landings coming from aggregations. Of 21 different aggregation areas noted in 1884, (Vilaro Diaz, 1884) (Table 1B), just one (Banco de Jagua, Oceanic bank off Cochinos Bay) still forms today (Claro[15]).

Annual landings records are not available from the Cayman Islands, although reports from fishers in the 1980s indicated that aggregation catches were declining from previous levels (Bush[42]). Data from the 1990s indicate that few fish were caught at aggregations in 1997 and 1998, although bad weather may have been partly to blame (Bush[42]).

Central and South America In Belize, where more than 30% of all grouper landed are Nassaus, catches from aggregations declined about 50% from 12,200 kg per year to 5,900 kg over a 10-year period ending in the late 1980s (Carter 1988, 1989), while total annual landings declined from 90,900 kg in 1984 to 21,000 kg in 1991 (Sadovy, 1997). In Mexico, one traditional aggregation, known since 1910–20, attained commercial im-

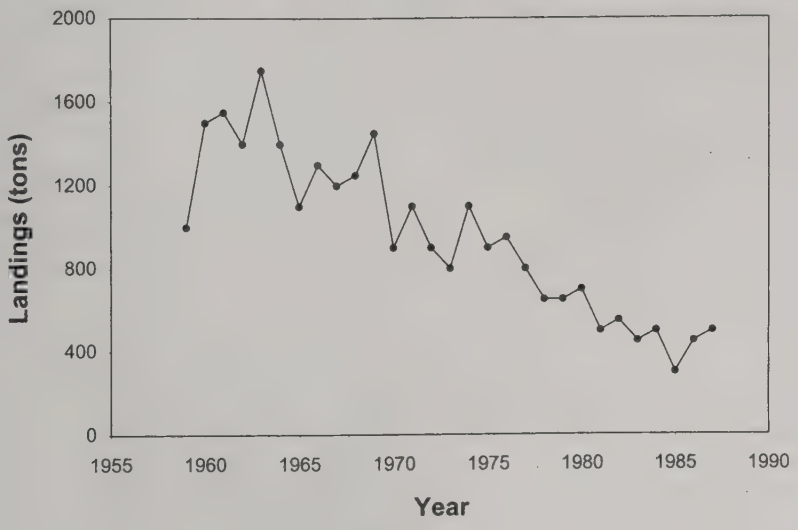

Figure 34
Mean annual landings (in tons) of Nassau grouper, *Epinephelus striatus*, in Cuban ports between 1959 and 1988 (modified from Claro et al., 1990).

portance in the 1950s but by the end of the 1960s aggregation numbers had declined (Aguilar-Perera, 1994). An aggregation site in Honduras that produced catches of 17,000 to 20,000 fish in early 1988 dwindled to about 500 fish by 1991 following intensive fishing in the intervening years (Fine, 1990, 1992).

Landings from Colombia peaked in 1986 and then dropped dramatically in 1987. Although landings increased from 1987 to 1991, they were still less than half of those reported for 1986 (FAO, 1993) (Table 20).

Florida U.S. commercial landings data for Nassau grouper became available in 1986 when this species was first distinguished from other groupers in the catch. From 1986 to 1993, Atlantic coast landings declined from 4,400 kg to less than 1,400 kg, and Gulf of Mexico landings fluctuated widely, peaking in 1990 at 4,100 kg (Fig. 35).

Recreational catches of Nassau grouper, including fish caught and released, have fluctuated widely since first recorded in 1979. In the Gulf of Mexico, landings peaked at almost 135,000 individuals in 1984, dropping to below 90,000 in the early 1990s (Table 13). The U.S. Atlantic coast recreational fishery showed a dramatic trend, with a total catch of over 100,000 fish in 1979, declining to less than 11,000 from 1986 onwards (Table 13).

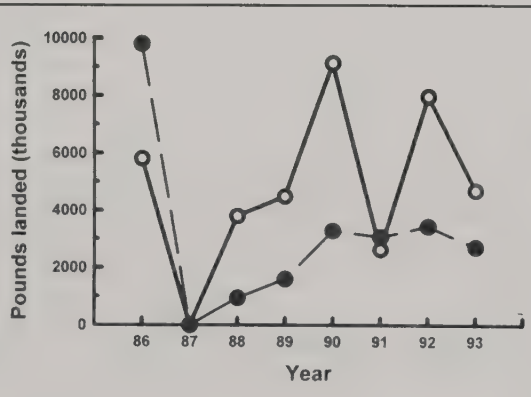

Figure 35
U.S. commercial landings, in pounds, of Nassau grouper, *Epinephelus striatus*, from 1986–93 in the Gulf of Mexico (white circles) and the Atlantic (black circles) (NMFS General Canvass Landings System).

Epinephelus itajara Few data are available for the jewfish, with limited information coming only from Florida for commercial and recreational catches. In the 1960s, Gulf of Mexico commercial landings of jewfish were mainly incidental to the snapper fishery of Yucatan (GMFMC[9]). In the U.S., from 1979–88, commercial catches increased from about 34,000 lbs (15,454 kg) to 136,000 lbs (61,818 kg) and then declined drastically (Fig. 36, Table 14). Although 5,000–17,000 fish were once taken recreationally each year, by the early 1990s less

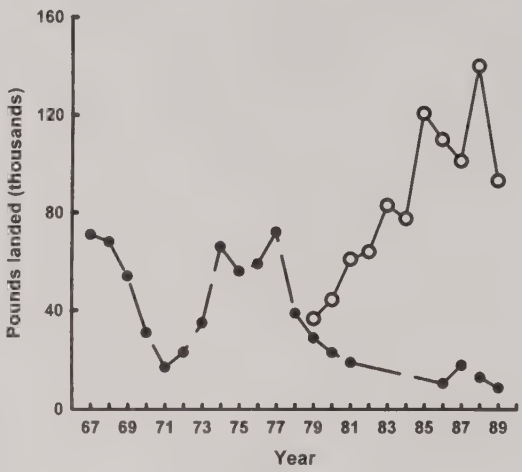

Figure 36

U.S. commercial landings, in pounds, of jewfish, *Epinephelus itajara*, from 1979–89 in the Gulf of Mexico (white circles) and from 1967–81 and 1986–89 in the Atlantic (black circles) (data from 1979–85 for the Gulf of Mexico are from Gulf of Mexico Fishery Management Council 1990; data from 1967–81 for the Atlantic are from South Atlantic Fishery Management Council, 1983; data from 1986–89 are from NMFS General Canvass Landings System).

than 5,000 were caught and released annually (Table 15).

In the U.S. Atlantic, commercial jewfish landings from Florida totaled 19,000 lbs (8,600 kg) in 1981, representing an almost fourfold decline from 1974–77 when about 70,000 lbs (31,818 kg) of jewfish were taken (SAFMC[24]) (Fig. 36). Annual catch declined almost every year after 1981 until a total ban was implemented in 1990 (Fig. 36). Recreational catch in the Florida-Atlantic has remained very low, with catches of over 1,000 fish recorded in only three years out of the past 15 (Table 15).

A commercial fishery for jewfish still exists at aggregations off Belize, although landings have declined since the 1960s when the fleet modernized and expanded (Wells[33]). No landings data were available.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory measures

Nassau grouper and jewfish characteristics of slow growth, large size at sexual maturation, site-specificity, and concentrated spawning events make them highly susceptible to overexploitation. They are among the largest members of multi-species fisheries, and even juveniles are highly susceptible to the fishing gears typically used. For example, in Puerto Rico the mean weight of all fishes taken with fish traps is 0.3 kg, well below the 1.9 kg of a Nassau grouper at sexual maturity (Sadovy, 1993). It is evident that these groupers cannot sustain fishing pressure beyond light levels and that in many areas aggregations disappear either soon after discovery or when fishing effort increases over traditional low levels, either directly on aggregations or on local stocks (Sadovy 1994, 1997). The most effective management approaches are likely to be protection of spawning aggregations and conservation of juvenile and adult biomass through marine reserves in suitably selected habitats.

Epinephelus striatus Most range states have implemented increasingly restrictive regulatory measures for the Nassau grouper over the last 10–15 years as landings declined (Table 21). For example, in the U.S., the GMFMC initially imposed a 20 inch TL (510 mm) size limit, a 5 fish recreational aggregate bag limit on groupers, and a 11.0 million lb (4,500,000 kg) commercial quota for all groupers combined (excluding jewfish) (GMFMC[38]). In 1983, the U. S. SAFMC specified a 12 inch (305 mm) minimum size limit for Nassau grouper, based on a yield-per-recruit analysis done on the closely related red grouper, *Epinephelus morio* (since insufficient data were available for the Nassau grouper); the analysis indicated that the Nassau was growth overfished (SAFMC[24]) and that the maximum sustainable yield required a size limit of 24 inches TL (610 mm), at the 1983 level of fishing effort.

Other management actions included a change in the fish trap mesh size to greater than 1.5 inch (38.1 mm) hexagonal and a prohibition on trawling of reef fish between North Carolina and Cape Canaveral (SAFMC[24]). Nonetheless, by 1991 the SAFMC felt that Nassau grouper was severely overfished and that all retention should be prohibited (SAFMC[46]). In 1996, the GMFMC followed suit and proposed a moratorium on Nassau capture (GMFMC[47]). The species is now protected in all U.S. waters.

In 1985, the CFMC instituted a 12 inch TL (30.5 mm) minimum size limit for Nassau grouper, to be increased by 1 inch (25.4 mm) increments each year to achieve a 24 inch (609.6 mm) limit by the mid-1990s (CFMC[30]). Surveys at the time indicated that 31% of Nassau grouper landed were less than 12 inches, with almost 100% less than 24 inches (CFMC[30]) (Fig. 22). By 1990, the capture of Nassau grouper had become a rare event in

[46] SAFMC. 1991. Amendment Number 4, Regulatory Impact Review, Regulatory Flexibility Analysis and Environmental Assessment for Fishery Management Plan for the Snapper Grouper Fishery of the South Atlantic Region, 87 p.

[47] GMFMC. 1996. Amendment #14 to the Fishery Management Plan for the Reef Fish Fishery of the Gulf of Mexico, 85 p.

Table 21

Management measures in effect in 1997 for Nassau grouper and jewfish. The location of the measure, the date of its implementation, and the type of measure are given. U.S. state waters in Florida are from the coast to 3 miles to the east (Atlantic) coast and 9 miles to the west (Gulf of Mexico) coast.

	Location and date measure implemented	
Measure in effect (1997)	Nassau grouper	Jewfish
Quota	Cuba mid-1980s	
Minimum size	U. S. Gulf of Mexico (1989) 510 mm TL Bahamas 1.36 kg	
Gear restriction	Mexico (1993) speargun banned and (1995) gillnet banned at Mahahual aggregation Cayman Is (1985) only lines at aggregations Belize gear restrictions at aggregations	
Moratorium	U.S. Atlantic (1991) U.S. Caribbean (1990) Bermuda (1996) Dominican Republic (mid 1980s) no catch or sale of ripe females in spawning season U. S. Gulf of Mexico (1997)	U.S. Gulf of Mexico & Florida State (1990) Caribbean Council (1993) U.S. Virgin Islands territorial waters (1993) U.S. Atlantic (1990)

U.S. Caribbean waters, indicating severe overfishing, and the CFMC prohibited any take or possession of this species in 1990 (CFMC[48]). Because most exploitation is within territorial waters, the U.S. Caribbean territories were asked to extend the reef fish federal regulations to shore (Appeldoorn et al., 1992). As of 1997, the territories had not yet complied with that measure.

Minimum sizes, protection, and quotas have been introduced elsewhere (Sadovy, 1994). In the Bahamas, a minimum of 1.36 kg is permitted and one aggregation site was first protected in 1999 (Ray[43]). In Cuba, in the mid-1980s, a quota was introduced on take of Nassau grouper (Claro[15]). In Bermuda, there is a moratorium on capture (Luckhurst[49]).

Other measures aim to protect aggregating animals through gear restrictions or fishing prohibitions. In Mexico, for example, spearguns have been prohibited at aggregations since 1990 (Sosa-Cordero and Cárdenas-Vidal, 1997). Fishing for all groupers is also prohibited at aggregation sites in Bermuda (Sadovy, 1994). In the Dominican Republic, no fishing of serranids is allowed during spawning seasons anywhere and no marketing of ripe females is permitted (Bohnsack[1]). In the Cayman Islands, there are at least five aggregation sites; in 1985 three major sites were closed to fishing except for residents using handline (Tucker and Woodward, 1993; Bohnsack[1]). In Belize there are also gear restrictions at spawning aggregations (Perkins, 1983).

Epinephelus itajara The rapid increase in fishing effort for jewfish followed by the dramatic decline in catches led to extreme regulatory measures by the GMFMC. In 1989, the GMFMC approved a 50 inch (1,270 mm) size limit for jewfish (GMFMC[38]). This measure was originally considered conservative enough to restore jewfish stocks. However, reports that stocks were much more depleted than previously indicated led to Amendment 2 of the Gulf of Mexico Reef Fish Fishery Management Plan in 1990 which prohibited all capture of jewfish in federal Gulf waters (GMFMC[9]). It was the Gulf Council's opinion that, without a moratorium, jewfish would become threatened or endangered (GMFMC[9]). In 1990, the SAFMC followed the actions of the GMFMC and enacted an emergency rule prohibiting the take or possession of jewfish in U. S. federal waters.

The CFMC prohibited the capture of jewfish in 1993, stating that the abundance of jewfish had declined throughout the U.S. Caribbean, and, possibly, throughout much of the Caribbean (CFMC[29]). The U.S. Virgin Islands' territorial government also made jewfish a protected species, allowing no take in territorial waters (CFMC[29]).

The State of Florida banned the capture of jewfish in 1990. Prior to the ban, the size limit on jewfish was 18 inches (457 mm) in Florida waters. Although jewfish are rarely caught in the Atlantic north of Florida, there are regulations restricting the take of this species from spe-

[48] CFMC. 1990. Amendment Number 1 to the Fishery Management Plan for the Shallow-water Reeffish Fishery, Preliminary Environmental Assessment and Regulatory Impact Review, 10 p.

[49] Luckhurst, Brian. 1996. Dept. Agriculture, Fisheries and Parks, Government of Bermuda, P O Box CR52, Crawl CR BX, Bermuda. Personal commun.

cial management zones around artificial reefs off South Carolina and Georgia.

6.2 Environmental changes

Epinephelus striatus* and *E. itajara The increase in urban, industrial, and tourist developments throughout these species' ranges impacts coastal mangroves, seagrass beds, estuaries, and live coral (Mahon, 1990), reducing the availability of suitable juvenile and adult habitat. Loss of juvenile habitat, such as macroalgae and seagrass beds for the Nassau grouper and mangroves and estuarine habitats for the jewfish, is likely to negatively affect recruitment rates. Physical damage to spawning sites could potentially impact reproductive activity if alternative sites are not acceptable.

Seawater temperature changes, as from global warming, could affect reproduction, since this appears to be temperature specific (25–26°C), at least in the Nassau grouper (Section 4.32).

6.3 Regulatory strategies

Epinephelus striatus* and *E. itajara Management agencies have generally sought to minimize growth and recruitment overfishing and to preserve the spawning stock biomass per recruit (SSBR). Minimum size limits address growth overfishing and increase yield per recruit, while the protection of reproductive adults reduces recruitment overfishing. The SAFMC[10] determined that SSBR should be maintained above 30% for Nassau grouper and above 40% for jewfish to prevent recruitment overfishing (i.e. stocks should be maintained at 30–40%, respectively, of their virgin spawning stock biomass) (Goodyear, 1993). The South Atlantic Fishery Management Plan Development Team (PDT[50]) believed that the SSBR for Nassau grouper was probably less than one percent, and both the SAFMC and the GMFMC concluded that jewfish had been fished far below the 30% SSBR level. The GMFMC[9] suggested that even with a 50 inch (1,270 mm) size limit on jewfish, jewfish SSBR would be 11% or less, depending on release mortality, which was believed to be high. With release mortality assumed to be 50%, SSBR was estimated at 1.3%. At such a low SSBR, stock depletion seemed imminent for both species and emergency rules were implemented in 1990 (Section 6.1).

In the Caribbean, funds for management are limited (Mahon, 1993) and, given the small-scale, multi-species nature of the fisheries, single species management is precluded. More general management approaches, however, can reduce capture of immature individuals and benefit both the Nassau and jewfish. In Cuba, Puerto Rico, and elsewhere, for example, increases in trap mesh sizes were proposed to reduce take of immature individuals (Baisre, 1993; CFMC[26]). The FAO recommended in 1990 that the Lesser Antilles institute fishing licenses to limit entry and allow declines in effort through attrition, as well as enforce prohibitions of damaging fishing gears such as entangling nets and dynamite (Mahon, 1990).

Marine reserves and closures promise to be excellent approaches to the management of reef fish species that are relatively site-attached, like groupers, or depend on critical habitat at some life history stage (Roberts and Polunin, 1991; PDT[51]). Belize and the Netherlands Antilles have established marine parks with fishing closed in certain zones within the parks (Polunin and Roberts, 1993). There are marine parks in state and federal waters off Florida, although only one, Florida Keys National Marine Sanctuary, includes no fishing zones (implemented in 1997). In 1986, the Exuma Cays Land and Sea Park in the Bahamas prohibited all take and appears to effectively protect Nassau grouper biomass; reproductive output (eggs per hectare) was over six times inside than outside this park, because of the protection afforded (Sluka et al., 1997b). Mean number of jewfish spawners increased after a 1990 fishery closure (Fig. 27).

In the early 1990s, due to concern over the status of these two species, both were named as candidates for the United States Endangered Species List and both now appear on the 1996 Red List of the International Union for the Conservation of Nature (Hudson and Mace, 1996). There are moratoria for both groupers in U.S. and Bermuda waters.

7 AQUACULTURE

Epinephelus striatus

The Nassau grouper is considered a prime species for aquaculture since it is a popular and valuable food fish and stocks are severely depleted (Tucker, 1992a, 1992b). In recent years, considerable progress has been made in hatchery spawning and rearing of groupers under aquarium conditions (Tucker, 1992a; Watanabe et al., 1995a, 1995b; Tucker et al., 1996).

Female Nassau groupers were induced to ovulate using human chorionic gonadotropin (HCG) injections, luteinizing hormone-releasing hormone analog (LHRHa), and carp pituitary homogenate (CPH), or combinations thereof (Tucker, 1992b; Kelley et al., 1994; Watanabe et al., 1995a). Females with mean oocyte diameters rang-

[50] Plan Development Team (PDT). 1990. South Atlantic reeffish: Plan Development Team report to the South Atlantic Fishery Management Council, 527 p.

[51] PDT. 1990. The potential of marine fishery reserves for reef fish management in the U. S. southern Atlantic. NOAA, NMFS, Coastal Resources Division, Contr. No. CRD/89-90/04, p. 41.

ing from 482–561 micrometers were suitable for hormone-induced spawning (Watanabe et al., 1995a). Tucker et al. (1996) described four methods for achieving fertilized eggs, including combinations of induced or natural ovulation and artificial fertilization with fresh milt or natural spawning in tanks.

Fertilization rates in artificially induced spawns ranged from 18–100% and hatching success ranged from 68–100% (Head et al., 1996; Tucker et al., 1996). Multiple spawns occurred on consecutive days and hatchery-reared juvenile Nassau groupers grew to 1.5–2.0 kg in 2 years (Tucker and Woodward, 1993).

Larval survival to first feeding can be high, with declines thereafter depending on feeding regime. Survival of larvae to first feeding in one set of experiments was 65% (Tucker, 1992b) but was found to decline to about 1% by day 62 post-hatching in another (Watanabe et al., 1996); larval survival declined once the yolk sac was absorbed. Feeding with oyster trochophores and sieved rotifers, combined, achieved higher larval survival rates than feeding with unsieved rotifers alone (Watanabe et al., 1994) and small prey size was important (Watanabe et al., 1996). Results of feeding experiments indicated that cultured juveniles require a dietary protein level above 55% and an energy to protein ratio of below 28.9 kJ/g for optimum growth (Ellis et al., 1996). Control of turbulence, salinity, and light intensity can improve survival to the first-feeding stage (Ellis et al., 1997a). Increased growth and feeding rates occurred with increased water temperatures (Ellis et al., 1997b).

Following hormone injections, Nassau grouper females produced clutches of between 23,000 and 600,000 mature eggs per kg of body weight, with large females capable of yielding almost 5,000,000 eggs. Kelley et al. (1994) reported one to two clutches produced during the natural reproductive season, with each clutch totaling 50,000–600,000 eggs per kilogram body weight. Head et al. (1996) found that females could spawn two to three times at intervals of 28 to 75 days, producing 200,000–2,000,000 eggs per female (54,000 and 340,000 eggs/kg body weight) with females ranging in size from 3.5–6.8 kg. Tucker et al. (1991) noted clutches of 500,000 to 700,000 for females ranging from 3–5 kg (166,666 to 140,000 eggs/kg), while Watanabe et al. (1995a) reported stripped females of 4.2–12 kg releasing between 95,000 and 4,750,000 eggs (22,619–395,833 eggs/kg), with a significant relationship between body weight and eggs stripped ($y=0.385x-0.5589$; $r^2=0.40$, $n=41$, $p<0.001$; y is eggs stripped and x is body weight in kg).

Experiments are underway to determine the success rate of larval Nassau grouper culture and survival of released hatchery-reared juveniles (Roberts et al., 1994; Watanabe et al., 1995a, 1995b). Although temperature manipulation might be used to condition Nassau grouper to spawn any month of the year (Tucker et al., 1996), hatching success was higher between 26–28°C compared to hatching at 30°C (Watanabe et al., 1995b). Nassau grouper juveniles (309–367 mm TL) reared from eggs ($n=27$) were used to test the feasibility of restocking reefs (Roberts et al., 1994). Despite some mortality and dispersal, a few tagged fish were observed up to nine months after release. The potential of Nassau grouper stock enhancement, as for any other grouper species, has yet to be determined (Roberts et al., 1994); serious doubts about the genetic consequences of introductions and about possible problems of juvenile habitat availability, introduction of maladapted individuals, or inability to locate traditional spawning aggregations, continue to be raised. Certainly aquaculture and stock enhancement are not solutions to overfishing or species endangerment and are no excuse for avoiding management of vulnerable and overfished fishery resources.

Epinephelus itajara

The jewfish, like the Nassau grouper, is considered to have prime aquaculture potential (Gomez-Gaspar and Cervigón, 1987; Roberts, 1990). Wild juveniles have been raised experimentally on a fresh fish diet in floating cages in Venezuela (Cervigón, 1983).

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